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BULLETIN DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX

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VESPA DYBOWSKII ANDRÉ
AS A FACULTATIVE TEMPORARY SOCIAL PARASITE [1]

by

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Among the species belonging to the genus *Vespa* (or *Macrovespa* D. T. of Bischoff and Weyrauch), *Vespa dybowskii* André is conspicuous by the red-brown fore-body and uniformly black abdomen. Its geographic range extends over Siberia, Southern Ussuri, East China and Japan (Hokkaido (3) and Honshû). Except a brief note by Maa ('36) (4), however, no detailed informations have been hitherto published upon its habits. In Shimoina District, Nagano Prefecture, this hornet is rather scarce in number, but Fukushima could obtain, during about twenty years, miscellaneous knowledges on its life mode. As the results of observations, though yet incomplete, include several interesting facts, some of them will be described in the present paper.

In Central Japan, this species inhabits generally the mountaneous regions and rarely below ca. 300 m above the sea level in Nagano Prefecture. The emergence of hibernated queens begins in the middle part of May and continues over a relatively long period. The nesting sites preferred by them are hollow trees, apertures under roof-tiles, cavities in decayed beams, cracks in wooden or earthen walls, rocky crevices etc. Several examples are cited herewith:

Obs. 1 (at Yasunobumura): Inside a decayed foundation beam of a hen house. Corresponding to the narrow space, the nest was very slender, i. e., 10 cm in diameter and 30 cm in length. *Obs. 2 & 3 (at Shimojōmura):* In a narrow crack on the wall of an earthen storehouse and inside a decayed beam of the pent-roof of another. *Obs. 4 (at Yasunobumura):* Inside an earthen pan accidentally turned upside down on an indoor passage. *Obs. 5 (Komabamura):* In a rocky crevice situated about 3 m above the ledge surface. The adjacent crevices perfectly stuffed by wooden pulp.

Judging from these examples, together with other observations, it can be concluded that this hornet tends to prefer relatively narrow cavities above the ground, but neither free aerial situations nor underground cavities. A well developed nest consists of usually three combs, though their diameter seldom exceeds 20 cm. The fresh weight of a whole nest hardly reaches 1 kg generally. Hence this species builds the smallest nest among hornets inhabiting the District except *V. tropica* var. *pulchra* Buysson. Nest material not differs from those used by other hornets. Diameter of cells is mostly slightly less than 10 mm in queen cells, and fluctuates btw. 8-9 mm in worker ones. Perhaps partly caused by the narrowness of cavities employed, the arrangement of combs shows a peculiar irregularity. It is not always easy to distinguish clearly each comb, of which surface is also characterized by a marked unevenness.

The adults visit tree sap but are yet not found on flowers. They hunt rather indiscriminably insects of various sizes and forms. Even the quite large ones, such as crickets, grasshoppers, moths, dragonflies (except larger species such as *Anax*) are victimized by a jetting attack done at a distance of about 1 m apart from the prey. Like other hornets, they accept willingly the flesh of birds, snakes and frogs from the man's hand if these are offered after skinned. Mantids and large Assylids can be counted as the natural enemies. *Vespa dybowskii* is one of the most ferocious species among the hornets inhabiting the District. In observing their activities near the nest, the workers frequently attempt to attack the observer with a distinctly aggressive disposition.

It is well known that various species of hornets visit preferably tree sap and, at the places where the secretion is abundant, often claim the territorial right by chasing all the visitors of same or different species from the place. The dominance relation among different species is, though greatly influenced by the individual ability, relatively stable in a given region. In Shimoina District, the following order can be observed as an interspecific dominance relationship : *V. mandarinia* ≫ *V. dybowskii* > *V. analis* var. *insularis* > *V. crabro* > *V. xanthoptera* ≫ *V. tropica*. var. *pulchra*. This is comparable to the biological rank discovered by Hediger '40 among the related species of higher vertebrates. The power relation between two neighbouring species, however, not equivalent in each combination. The relations among species lower than *V. analis* var. *insularis* D. T. are sometimes indistinct in each encounter and often result a severe combat. On the other hand, *V. mandarinia* Smith tyrannizes perfectly over all other congeneric members. If a tree sap of abundant secretion is occupied by this species, other species except *V. dybowskii* usually tend to give away the place without fighting. Only *V. dybowskii* seeks the fluid without hesitation in the presence of *V. mandarinia*, and moreover, occasionally challenges the war to the formidable competitor, though it results in the majority her defeat and retreat.

In spite of the possession of perfect abilities to found an independent colony by her own hands, the queens of *V. dybowskii* seek preferably a

nest of *V. crabro* L. already established, and parasitize socially upon it.

This remarkable habit has not been recorded up to present. But, due to the clear difference of colour pattern between two species (fig. 1), it has been well known among the laymen of District that the banded workers in a *crabro* nest were gradually replaced by the markless workers of *V. dybowskii*. The process of invasion has been yet not observed. But the following observation may be very suggestive to imagine the course of usurpation.
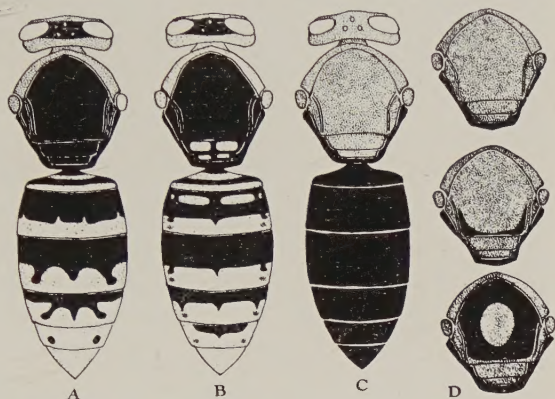
Fig. 1. — Colour pattern of host and parasite hornets. A. *Vespa crabro*, B. *V. xanthoptera*, C. *V. dybowskii*, D. Colour variation in thorax of *V. dybowskii*.

Obs.6 (Shimojômura): In one afternoon of early July, a great uproar was observed in a nest of *V. crabro* situated at a hollow kaki-tree. Numerous workers of *V. crabro* flew about the nest and frequently approached the observer with a decisive excitation. Thereafter the uproar declined gradually and ceased in the evening. A few weeks later, it was found that the workers of *V. dybowskii* began their activity side by side with those of *V. crabro*, but the latter decreased by and by during summer. In September, the nest was completely replaced by *V. dybowskii*.

No other informations which suggest the attack of *V. dybowskii* were obtained in the District. However, there are about twenty records in which the replacement of the nest of *V. crabro* by *V. dybowskii* was confirmed. Moreover, such the replacement was observed in two locations during several years successively. One example (*Obs. 7*) was seen at a hollow branch (ca. 20 cm in diameter) of an old pine, and the other (*Obs. 8*) at a hollow pine of about 12 m in height. In both cases, the cavities were utilized by V. crabro during 5-6 years. In the former case always, in the latter 2-3 times usurped by *V. dybowskii*.

DISC NO. (from above).	DIAMETER	NUMBER OF CELLS			DIAMETER of cells	NUMBER of auxiliary petioles
		complete	half-built	rudim.		
1	17 × 12 cm	405	38	—	7-8 mm (centrally), 8-9 (periph.)	5
2	13 × 11	154	15	7	9.5-10 partly 8-9	10
3	6 × 5.5	37	10	17	9-10	3

An example of the nest of *V. crabro* replaced later by *V. dybowskii* is illustrated in Figure 2. *(Obs. 9)*. The nest was taken in November after the extinction of the whole colony. It was situated in a narrow cavity under the barn-roof (about 6 m in height, Shimojômura) and consisted of three discs of which dimensions were as in the table.

Though not distinct in the photograph, the first and second combs are not perfect discs. There are some inconsistencies at their comb surface, consequently they show a tendency to build four layers which are arranged alternatively each other. It cannot be concluded, however, whether this irregularity represents the characteristic architectural technique of *V. dybowskii* or a mere adjustment for a limited space. The length of cells attains to about 3 cm when completed. There are no overgrown cells projected from the comb surface. Petioles are mostly round in their transverse section but become more or less flat when their diameter increases. The outer paper-cover is mostly omitted except a limited portion, a trait being common to both the host and parasite species when they nest in a dark, narrow space. In its general plan, the nest is so well integrated that there are no mosaic-structures suggesting the difference of architecture between two species. The nest is not unusally large if it is considered as the nest of *V. crabro*, but is larger than usual nests of *V. dybowskii* which were built independently.

Besides *V. crabro*, the nest of *V.xanthoptera* Cameron is occasionally invaded, also when it was built in a narrow cavity above the ground. One example is cited:

Obs. 10 (Shimojômura): A hollow walnut tree, ca. 20 cm in diameter, and ca. 1 m above the ground, was chosen in spring by a queen of *V. xanthoptera*. The nest developed successfully and activity of the workers was obvious judging from their frequent in- and outflies at the entrance. However, all the activities dissappeared suddenly. Some weeks later, the workers of *V. dybowskii* began their foraging activities at the same nest.

Based upon the obtained records, we can conclude as follows: *V. dybowskii* is amphipotential with respect to the nest foundation. In spite of her ability to found the nest independently, the queens of this hornet seek preferably the nests of *V. crabro*, or occasionally of *V. xanthoptera*, being already well established, and after intrusion utilize both the nest and the labour of the host workers to establish her own colony. The fate of the host queen is yet not ascertained. When the nests of *V. crabro* were examined after the complete replacement by *V. dybowskii*, they contain always only one queen of the latter species, but never that of the former. The marked aggressiveness of *V. dybowskii* was already mentioned. Hence, it may be assumed that the proper nest mother is sacrificed by the usurper at the time of invasion or soon later. In figure 3, various process of the colony development were illustrated schematically. The bipotentiality of *V. dybowskii* may be well recognized when the process I-II-III... (independent foundation) and i-ii-iii-iv-III... (dependent foundation) are compared. The above cited example, in which *V. dybowskii* attacked *V. xanthoptera*, is very interest, because the parasite seems to utilize, in such the case, only the results of the previous activities of the host, but not the future labour to be done by the host workers. A slight variation in the relative aggressiveness
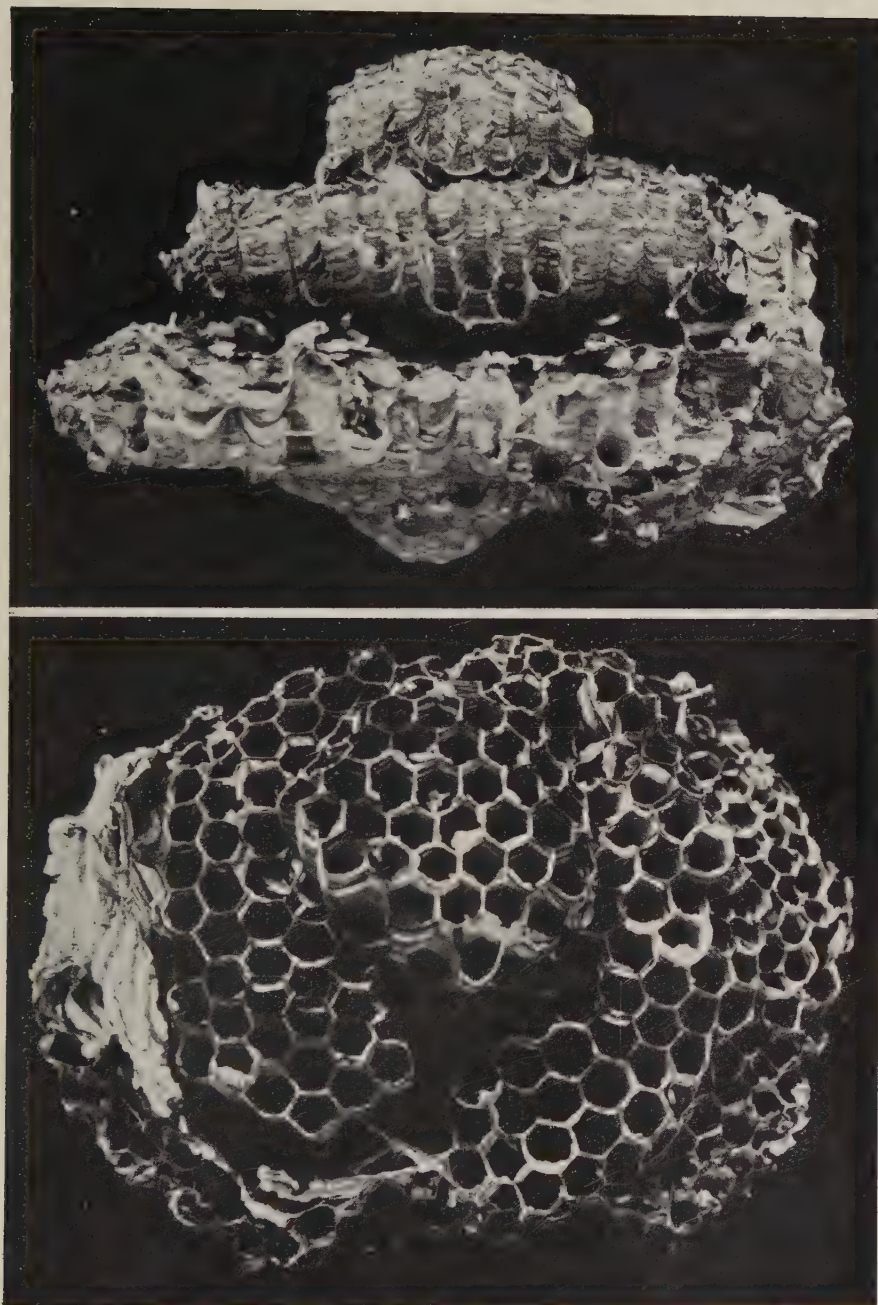
Fig. 2. — A nest of *Vespa crabro* later usurped and enlarged by by *V. dybowskii*

Table 1. Various phases of labour parasitism among social Hymenoptera

TYPE OF parasitism / taxonomic group	FACULTATIVE TEMPORARY		OBLIGATORY TEMPORARY		OBLIGATORY PERMANENT
	intraspecific	interspecific	without dulosis	with dulosis	(without worker caste)
	(1)				
Formicoidea	*Camponotus chilensis* (Goetsch und Kätner '38)		*Formica rufa* group and *F. exectoides* gr.→*F. fusca* *Crematogaster* spp. (*Oxygyne, Atopogyne*) → *Crem.* spp. *Lasius fuliginosus* → *L. umbratus* *L. umbratus* → *L. niger* etc.	*Formica sanguinea* → *F. fusca* *Polyergus* spp. → *F. fusca* *Strongylognathus* spp. → *Tetramorium caespitum* etc.	*Wheeleria* *Epœcus*→*Monomorium* *Epixenus* spp. *Symphheidole* *Epipheidole* *Parapheidole* → *Pheidole* spp. *Anergatus* → *Tetramorium* spp. etc.
				(mainly after Goetsch '53 & Wheeler '19)	
					(3)
Vespoidea	*Vespa crabro* (Janet '03) after Taylor '39 *Polistes ledwigae* (Yoshikawa '55)	*Vespula squamosa* → *V. rufa* var. *vidua* (Taylor '39) *Vespa dybowskii* → *V. crabo* and *V. xanthoptera*			*Vespula* (*V.*) *austriaca* → *V.* (*V.*) *rufa* *V.* (*Dolichov.*) *adulterina* → *V.* (*D.*) *norvegica* and *saxonica* *V.* (*D.*) *ingrica* → *V.* (*D.*) *silvestris* *V.* (*D.*) *tripunctata* → *V.* (*D.*) *media* var. *geeri* (Weyrauch '37)

		(4)
V. (D.) adulterina var. *arctica* → *V. (D.) arenaria* (Taylor '39) *Polistes sulcifer* → *P. gallicus* *P. semenovi* → *P. gallicus* (Weyrauch '37) *P. atrimandibularis* → *P. kohli* *Mischocyttarus fumiga-toides* → *M. 'umigatus* *M. graciloides* → *M. gracilis* and other 21 spp. of *Mischocyttarus* (Zikan '49)		*Psithyrus* spp. → *Bombus* spp.

Apoïdea	(2)
	Bombus (B.) terrestris B. (B.) terrestris → B. (B.) lucorum *B. (Lapidariob.) lapidarius* B. (B.) affinis → B. (B.) tricola *B. (Fervidob.) fervidu-* B. (F.) americanorum *B. (Pratob.) pratorum* → B. (Separatob.) separatus *B. (Subterraneob.) subterraneus* *B. (Fervidob.) americanorum* B. (Subt.) distinguendus → B. (S.) subterraneus (Plath '34, Frison '30, Richards '27, Reinig '35)

(1) Well known « adoption » of the queens of the same species is not listed.
(2) Requeening as an apicultural procedure evokes artificially the same result.
(3) There seems to occur much more parasitic Polistes, f. ex. *P. macrocephalus* from Belgian Congo and *P. perplexus* from N. America (Bequaert '40).
(4) Labour parasites of subsocial bees are excluded. (*Sphecodes*—*Halictus malachurus*, *Eucondylops* — *Allodape*.)

between the parasite and host may play an important role for such the
difference in the type of parasitism.

There are several suggestions to the fact, why *V. dybowskii* chooses
V. crabro and *V. xanthoptera* as the host species. The synchronization of
the queen appearance may be, without doubt, of the primary importance.
Among various hornets, only those species of which queens appear relativly
earlier than those of *V. dybowskii* may serve as the adequate substrata for
the forthcoming usurpation. Richards ('28) and Weyrauch ('37, '38)
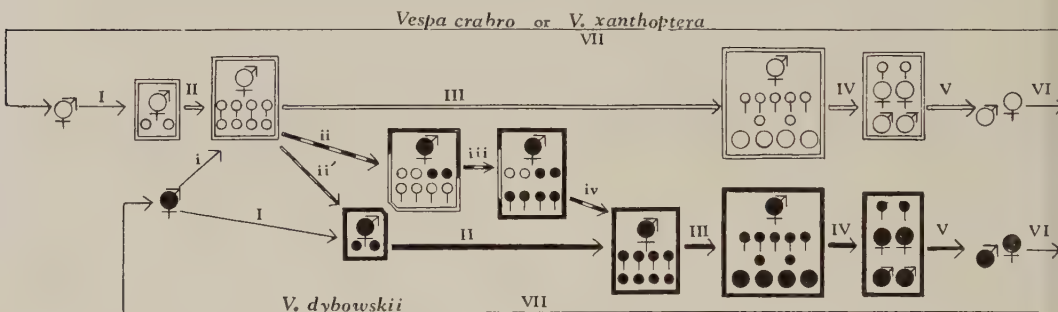asserted that the later appearance of queens with developed ovaries,

Fig. 3. — Schematic representation of various courses of colony development in host and parasite
hornets. I-II-III-IV-V-VI-VII : independent development. i-ii-iii-iv-III (or i-ii'-II-III-)-IV-
V-VI-VII : dependent development. ♂ fertilized queens, ♀ unfertilized queens, ♂ : males, ♀
workers, ○ : broods of queens and males, o : broods of workers, ▣ : nest (Black : parasite, White:
host, Bl. et Wh. : mixed state). I. independent nest foundation by fertil. hibernated queen,
II. developm. of colony and emergence of workers, III. further developm. of colony and pro-
duction of reproductive castes, IV. decline of colony and emergence of reproductive castes, V.
extinction of colony, VI. fertilization, VII. hibernation of fertilized queen, i. invasion of parasite
queen into a host colony, ii. appearance of mixed colony, iii. emergence of parasite workres,
iv and ii'.. complete replacement of host by parasite.

consequently with an increased urge in finding the suitable oviposition site,
can serve as an important factor to the incipient labour parasitism among
the social insects. In fact, the delayed appearance of queen in comparison
with that of host queen is observed repeatedly in facultative temporary
labour parasites (*Vespula squamosa*, Taylor '39; *Bombus terrestris*, Sladen
after Richards '34, *B. affinis*, Plath '34). In Shimoina District, the
seasonal sequence of appearance of hibernated queens in various hornets is,
though with a marked variation, generally as follows: *V. xanthoptera*—
V. crabro—*V. dybowskii*—*V. analis* var. *insularis*—*V. mandarinia*—*V.
tropica* var. *pulchra*. From this order, it may be readily assumed that
only *V. crabro* and *V. xanthoptera* are sufficiently qualified to be parasitized
by *V. dybowskii*.

Moreover, these two species offer the suitable conditions as the host
with respect to the degree of aggressiveness, the size of comb cells and the
nesting site chosen preferably. It is hardly expected that *V. dybowskii*
attacks the nest of *V. mandarinia*, being incomparablly ferocious and with
cells of larger size. *V. tropica* var. *pulchra* is relatively mild-tempted,

but its appearance is too late to be attacked by *V. dybowskii*. On the other hand, it must be solved by the further observations whether *V. analis* var. *insularis* D. T. can serve as the host species or not, though this hornet shows a marked aggressiveness.

The nests of *V. crabro* and *V. xanthoptera* are attacked by *V. dybowskii* only when the nests were built in a relatively narrow spaces above the ground level. This fact seems to indicate the important role of affinities in the nesting site between host and parasite. Up to present, no usurpation was recorded when *V. crabro* and *V. xanthoptera* built their nests in underground cavities or in aerial situations, with one exception which is worth citing herewith :

Obs. 11 (Shimojômura): One *V. crabro* nest built under a barn roof was later usurped by *V. dybowskii*, though the nest was situated in a relatively wide space. In autumn, at the fall of colony, the nest contained five combs, 45 cm in length but only about 20 cm in the maximal diameter. Hence, it showed an abnormally elongate shape. This is noteworthy because it suggests the probable innate tendency to build the nest with a small diameter, though this is determined in the most cases exogenously by the narrow space available.

Finally we should like to consider the life-mode of *V. dybowskii* in comparison with other phases of labour parasitism among social Hymenoptera, which are summarized in table 1.

The table is yet by no means complete. Especially in the obligatory parasitism of ants, only representative cases were cited mainly after Wheeler ('19) and Goetsch ('53) The classification itself must be revised if various factors are considered, namely, attitude of parasite towards the host queen (tolerant or not, if the latter is the case, the mode of tactics and time of the death of host), duration of colony (perennial or annual), degree of caste differentiation (mono-or polygyny) etc.

As seen in the table, *V. dybowskii* belongs to the facultative temporary parasite in the sense of Taylor '39. This type of labour parasitism is up to present relatively less mentioned than the obligatory one. Especially about the ants, the table shows clearly that our knowledges on this type are yet very scanty, in contrast to rich informations on the extreme differentiation in the obligatory parasitism (1).

Among other social insects, this type of social parasitism is well known in bumblebees (Sladen'12 after Reinig '35, Richards '27, Weyrauch '37; Plath '34). Especially in *Bombus* (*Bombus*) *terrestris* L., the later appeared hibernated queens tend frequently to invade the nest of the same species or allied one, *B.* (*B.*) *lucorum* L. Sladen recorded in one nest, about 20

(1) Authors' knowledges on the ant parasitism are, however, yet so incomplete that we are very glad if our probable shortcomings are corrected by other authorities. Moreover, there are instances which cannot simply classify in any of the categories mentioned. It is well known that many species of ants, in spite of their ability to found the nest independently, frequently thieve and rear the pupae of the same or occasionally different species, to make use them as the helpers for the future development of colony. Such cases are naturally not included in the table (As an extreme case, cf. Gösswald '32, relationship betw. *Camponotus ligniperda—Formica fusca*).

dead queens of this species, indicating frequent attempts to invade other nests already started. The examples among Vespoidea are yet very meagre. On the interspecific parasitism, only one case of *Vespula squamosa* (Drury) (Taylor '39) has been known until the present paper. On the intraspecific one, besides an old record in *Vespa crabro* (Janet '03 after Taylor '39), Yoshikawa ('55) recently described the usurpation observed between two queens of *Polistes fedwigae* D. T., but in this case the attack was done by a fecundated female of *superindividual stage*, in contrast to the ordinary cases, in which the usurpation occurs between two queens of the earlier stage. Therefore, as mentioned by the author himself, this case differs biosociologically from the ordinary labour parasitism in the social Hymenoptera.

Recently Shida ('53) reported in his comprehensive study of *Vespula lewisii* (Cameron), a strong interest expressed by the post-hibernated queens towards the nests of the same species already established. He assumed this phenomenon as a tendency to the incipient social parasitism. It may be conceivable that an urge for oviposition due to the developed ovaries causes such a behaviour.

It is well known that the obligatory social parasites are often characterized by a number of adaptive characters: Various trick devices in parasitic ants, or the development of chitinization, armature and stouter mandibles and sting in *Psithyrus* and parasitic *Vespula* or *Polistes*. Among those belonging to the facultative type, it is reasonable that such the specializations may be not so remarkable if any. After Weyrauch ('38), *Bombus terrestris*, which often parasitizes on *B. lucorum*, possesses more developed chitinization, sting and aggressiveness compared to her facultative host. It can be said, however, that these characters show yet by no means the results of a directed specialization. In our example, *V. dybowskii*, besides the unique colour-pattern and marked aggressiveness, is characterized by a peculiar odour and stronger chitinization. The latter peculiarity, which is especially distinct when a living specimen are examined and compared with other species of hornets, is considered without doubt as an adaptive character. The odour of this hornet resembles somewhat that of papilionid-caterpillars. It is distinct even in a single worker at a tree sap and very strong near the nest. It is yet not clear, however, whether this odour play any role in their tactics or not.

The peculiarity of this hornet lies further in the fact that the parasitic nest foundation is rather a normal process in this species. In examples of facultative parasitism cited in the table, the dependent nest foundation is recorded as abnormal cases. In *V. dybowskii*, the independent foundation was observed about 10 times, whereas the dependent type more than 20 times. Therefore, this hornet shows an interest tendency to approach the obligatory temporary parasitism, which is, as seen in the table, yet not discovered among the winged social Hymenoptera.

Among the bumblebees, both the intra- and interspecific parasitisms are found often in the same species (cf. table). But we have yet no records on

the intraspecific parasitism in *V. dybowskii*. Without careful observations, discovery of the intraspecific parasitism is surely very difficult especially in Vespoidea which build their nests in situations other than underground cavities. But it is also conceivable, that the marked aggressiveness of *V. dybowskii* is inconvenient for the intraspecific parasitism for both the host and parasite. Taylor ('39) considered the transition from the intra- to interspecific type as a necessary step in the development of social parasitism. This may be the most probable way but not always the unique one. After Eidmann '27 and Gösswald '38, there seem to occur various ways which lead the ants towards the social parasitism. There are instances in which the parasite is descended directly from the present host, as seen in *Mischocyttarus* spp. recorded recently by Zikán '49. It may be not always impossible, however, that the social parasitism begins with the interspecific relation, or tranfers soon from intra- to interspecific one by a rapid dissappearance of unfavorable intraspecific parasitism.

Summary.

Vespa dybowskii André can establish the nest either by the independent foundation like as other hornets, or by the usurpation of the nests of *V. crabro* L. or *V. xanthoptera* Cameron already established. Namely, this hornet belongs to the facultative temporary social parasite like as *Vespula squamosa* (Drury) and certain bumblebees. The marked aggressiveness of this hornet and other biological observations were described together with some considerations on the labour parasitism among the social insects.

Zusammenfassung.

Vespa dybowskii André kann ihre Nest falls durch die unabhängige Gründung wie andere Hornisse, falls aber durch die Oberung der schon gegründeten Nester von *V. crabro* L. oder *V. xanthoptera* Cameron, gründen. Nämlich gehört diese Hornis zum fakultativen temporären Sozialparasit wie *Vespula squamosa* (Drury) und gewisse Hummelarten. Die bemerkbare Kampflustigkeit dieser Hornisse und andere biologische Beobachtungen wurden zusammen mit einige Betrachtungen über die Arbeitsparasitismus in den sozialen Insekten beschrieben.

Résumé.

Vespa dybowskii André nidifie soit en construisant elle-même son nid comme les autres guêpes, soit en usurpant des nids de *Vespa crabro* L. ou *V. xanthoptera* Cameron déjà construits. Cette guêpe appartient donc aux

parasites sociaux temporaires facultatifs comme *Vespula squamosa* (Drury) et certains bourdons. On décrit ici l'agressivité marquée de cette guêpe ainsi que diverses observations biologiques, ce qui permet quelques considérations sur le parasitisme du travail parmi les insectes sociaux.

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THE SOLDIER MANDIBLES OF THE NASUTITERMITINÆ (ISOPTERA, TERMITIDÆ)

by

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INTRODUCTION

The mandibles of the soldier caste of termites of the subfamily Nasutitermitinae show considerable modification and reduction corresponding with the development of the nasus as an alternative means of defence.

The form of the soldier mandibles was used as a basis for classification by Hare (1937), and to a lesser degree by Holmgren (1911-1912) and Ahmad (1950).

The purpose of this study has been to investigate further the value of soldier mandibles in the taxonomy of the Nasutitermitinae and to relate them to the systematic arrangement of the subfamily as suggested by Ahmad (1950) on the basis of the imago-worker mandibles.

The present work is based mainly on species in the collection of the British Museum (Natural History), kindly made available by the Trustees. Thanks are also due to Dr. A. E. Emerson of Chicago for providing material of two species of *Eutermellus*. Other material came from the collection of the Colonial Termite Research Unit.

All examinations and drawings have been made from the under surface of the head, with the result that the drawings are reversed (i. e. the "left" mandible appears on the right hand side). This has been done for two reasons—to facilitate the examination of mandibles and comparison with the drawings, and to achieve uniformity where shortage of material has necessitated that mandibles should not be removed from the head for examination. In figures 3 and 5, a row of asterisks is inserted between certain genera. These are placed where the ascending order of evolutionary status, followed in arranging the drawings, is interrupted by the occurrence of subsidiary branches of the hypothetical phylogenetic tree.

SYSTEMATIC SECTION

The subfamily Nasutitermitinae is characterised by the progressive development of the frontal area of the head of the soldier caste into a protruding tubelike process or nasus. This nasus terminates in the fontanelle or opening of the frontal gland, and its development is coincident with the reduction of the mandibles, in contrast to the variation in soldier mandibles encountered in the other subfamilies. This reduction mainly affects the apical blade part of the mandible, which is eventually lost completely. The molar region, though greatly reduced, still retains, races of ts functional structure even in the most specialised forms
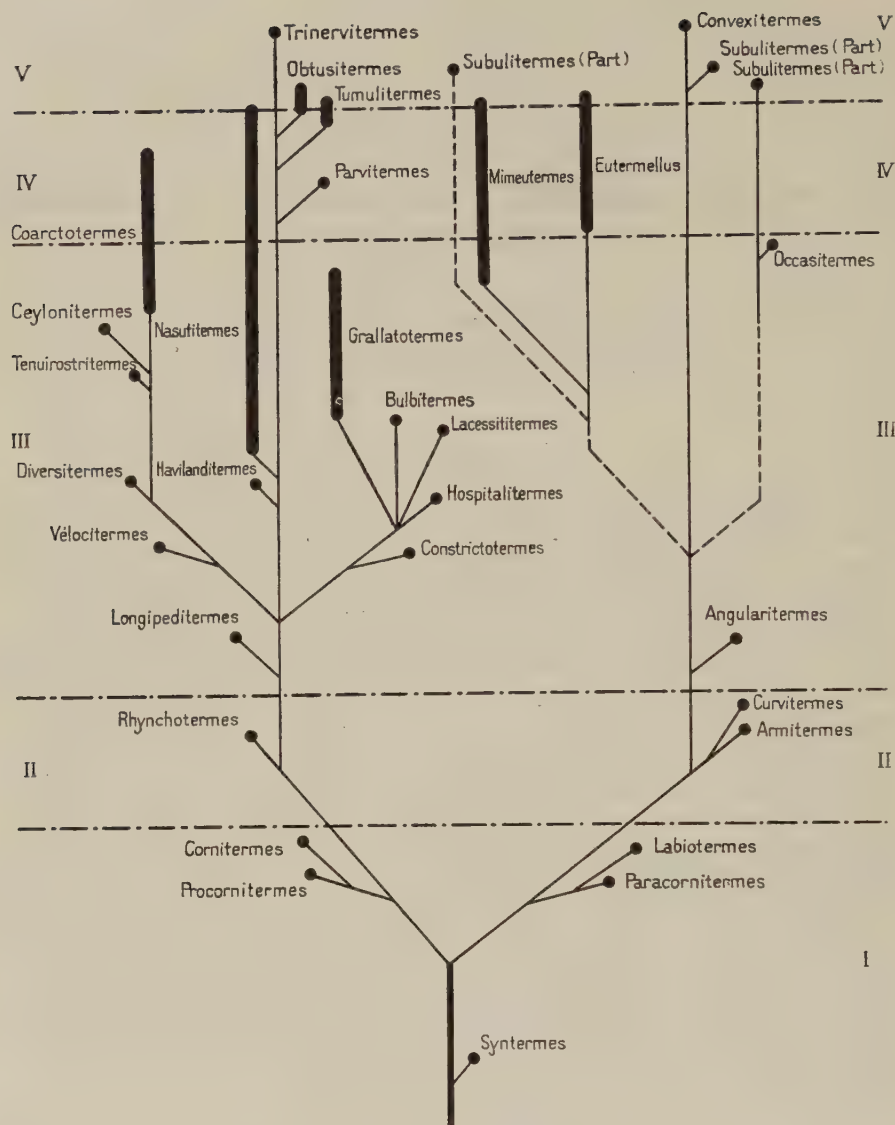
Fig. 1. — Hypothetical phylogenetic tree of the termite subfamily Nasutitermitinae. The Roman numerals arranged vertically mark stages in the reduction of soldier mandibles: I, Normal fully mandibulate soldiers. II, Nasute soldiers with large hooked mandibles, III, Nasutes with "blade" of mandible reduced to a conical "point" sometimes with a marginal tooth. IV, Nasutes with much reduced mandibles, "points" vestigial. V, Mandibles reduced to a simple lobe, "points" absent.

The genus *Syntermes* (fig. 3, A.) is generally regarded as the most primitive member of the subfamily. The soldiers have simple biting mandibles with a strongly hooked apical tooth, a less well developed marginal tooth, and a basal molar region. They are therefore basically similar to the more primitive termites.

According to EMERSON (1952): "One may postulate that an extinct group between *Syntermes* and *Procornitermes* gave rise to *Procornitermes* and *Cornitermes*. *Procornitermes* is more closely related to this extinct group. . . . . . *Rhynchotermes* probably arose either from this extinct group or directly from *Procornitermes*.

The *Paracornitermes-Subulitermes* branch probably arose from this extinct group. . . . . . and ultimately gave rise to a soldier which is strikingly similar to that on the *Nasutitermes* branch".

Thus the division of the Nasutitermitinae into two parallel branches is thought to have taken place before the development of the nasus and the reduction of the mandibles associated with it. These two main branches

Fig. 2. — Homology of the reduced soldier mandible of the Nasutitermitinae (diagrammatic). A, Worker caste (*Angularitermes*). B, Normal soldier caste (*Syntermes*). C, Reduced soldier caste (*Angularitermes*). D, Greatly reduced soldier caste (*Occasitermes*).

will be referred to by the name of the most primitive genus in each, that is, the *Procornitermes* branch (figs. 3 and 4) and the *Paracornitermes* branch (fig. 5). This division is shown near the bottom of the hypothetical phylogenetic tree in fig. 1.

The ultimate reduction of the soldier mandible to a rather feebly chitinised lobe occurs in both branches of the subfamily. It remains articulated with the head capsule by both the ginglymus and condyle, and still bears traces of muscle attachments. A very weakly developed molar surface is present.

While the nasute soldier-form is thus considered to have evolved independantly in each of the two branches of the subfamily, the subsequent reduction of the mandibles would appear to have taken place along a number of approximately parallel lines of evolution. The last stage of reduction has probably been reached at least four times, and is represented in the *Procornitermes* branch by *Trinervitermes* (fig. 4, L). The relationship of the genera is less clear in the *Paracornitermes* branch, since several members have the mandibles reduced to simple lobes, namely *Subulitermes*, *Convexitermes*, *Mimeutermes*, and *Eutermellus* (fig. 5, G-L). These probably cover three parallel lines of evolution, more or less related, which have all reached approximately the same stage.

In some of the most reduced mandibles a thinner patch of cuticle has developed at the apex of the lobe. This can be seen as a paler coloured

area in surface view, and may be some kind of sensory region. It occurs both in *Trinervitermes* and in *Convexitermes*, and is therefore a feature common to both the main branches of the subfamily. There are many intermediates between the normally mandibulate soldier without a proper nasus, and the fully nasute forms with reduced mandibles. The nasus developed before the reduction of the mandibles began, since there are nasute fully mandibulate soldier in both branches, *Rhynchotermes* (fig. 3, D) in the *Procornitermes* branch, and *Armitermes* and *Curvitermes* (fig. 5, C-E), in the *Paracornitermes* branch. In both branches at this stage the mandibles are somewhat bizarre in shape, probably indicative of a reduction in their importance for biting or snapping.

The most primitive genera known after the fully mandibulate forms already have the mandibles considerably reduced. The apical and marginal teeth (EMERSON, 1933), which form the blade part of the generalised soldier mandible, are reduced in these forms to an elongate conical process, which, in some cases, retains a small marginal tooth. The molar plate may bear one or more small teeth. Figure 2. illustrates the probable homology of the parts of these and still more reduced mandibles, the blade vestiges of which are commonly referred to simply as "points". In the *Procornitermes* branch the most primitive genus with this type of mandibles is *Longipeditermes* (fig. 3, E), which sometimes retains minute marginal teeth, particularly in the minor soldier. Approximately equal in status in the *Paracornitermes* branch is *Angularitermes* (fig. 5, F) which has a small marginal tooth on one or both mandibles, commonly on the right, and a small molar tooth on the left.

The *Procornitermes* branch has the greater number of intermediates between the semi-mandibulate forms and the final stage of reduction, and these fall into several parallel lines of evolution.

The *Paracornitermes* branch has very few intermediates, and because of the uncertainty of the relationship between the existing genera, will be described in a separate section.

The Procornitermes branch.

The stages of the progressive reduction of the soldier mandible are well illustrated by the *Procornitermes* branch. In the genus *Longipeditermes*, the points of the mandibles are fairly broad at the base, and take the form of elongate conical processes, which still constitute quite a substantial part of the mandible.

The next stage has already progressed considerably in the attenuation of the points to become minor appendages of the mandibles. *Velocitermes* (fig. 3, F) is the most primitive existing genus of this type, since it retains a small marginal tooth on one or both mandibles, and a well developed molar tooth. It is the lowest member of one of the secondary branches of the *Procornitermes* group, a branch in which the soldier mandible bears a molar tooth even in the most specialised genus, and the points taper sharply outwards from about half their length. In *Velocitermes* the marginal

tooth arises from the point where this taper begins, and its shape in the other genera suggests a tendency to retain a trace of such a tooth throughout the branch. *Velocitermes*, although it has points of the more specialised slender form, exhibits certain features, such as the marginal and molar teeth, in which it is at least as primitive as *Longipeditermes*, suggesting parallel evolution rather than linear descent.

The points are somewhat reduced in *Diversitermes*, (fig. 3, G) and are more so in *Tenuirostritermes* (fig. 3, H). All the remaining stages in the loss of the blade vestiges are represented in one genus, *Coarctotermes*. In *C. coarctatus* (Sjöst.) (fig. 3, I) they are only slightly more reduced than in *Tenuirostritermes*.

In *C. clepsydra* (Sjöst.) (fig. 3, J.) they are short and stout, and they become vestigial or absent on one or both mandibles in *C. tenebricus* (Silv.) (fig. 3, K.).

The distinct molar teeth which all these forms possess have been lost in *Ceylonitermes* (fig. 3, L.), which was placed by AHMAD in this branch on the basis of characters other than the soldier mandibles, and which may in fact be more closely related to the *Hospitalitermes-Grallatotermes* group of genera.

A second subsidiary branch which to some extent parallels the *Velocitermes-Coarctotermes* series is composed of the "constricted-headed genera". These show some distinct differences from the branch just described. Only in one genus is a molar tooth present on the soldier mandible, namely *Constrictotermes* (fig. 4, A.) and this has lost the marginal tooth. The imago is rather more specialised than the structure of the soldier mandibles would suggest, and the status of *Constrictotermes* must therefore remain somewhat doubtful. It could be regarded as a divergent form arising from the *Velocitermes* branch. None of the other genera in the group normally have either molar or marginal teeth, though in most cases the molar plate is roughened or ridged. The points taper much more evenly from base to apex than in the *Velocitermes* series.

The reduction of the blade vestiges does not reach so advanced a stage in this branch. *Hospitalitermes* (fig. 4, B.) is slightly more primitive than *Lacessititermes*, *Bulbitermes*, and *Grallatotermes* (fig. 4, C, D, E.) which are all at a stage approximately equivalent to *Tenuirostritermes* in the *Velocitermes* branch. The most specialised member of the group is the only African species of *Grallatotermes*, *G. africanus* Harris (fig. 4, F.) which has diverged somewhat from its congeners in having almost lost the points. These vary considerably from vestigial in some specimens to quite well developed in others. In addition, it has developed the thin patch of cuticle at the apex of the mandible seen in *Trinervitermes* and *Convexitermes*.

In the third of the secondary branches of the *Procornitermes* main branch, there are few intermediate forms between the most primitive and the most specialised. Nearest to the lower end of the scale is *Havilanditermes* (fig. 4, G) with well developed points, but no molar or marginal

C. *Cornitermes.*

F. *Velocitermes.*

B. *Procornitermes.*

E. *Longipeditermes.*

A. *Syntermes.*

D. *Rhynchotermes.*

Fig. 3. — Soldier mandibles of the Nas[...]

teeth. The next stage represented has vestigial points or none at all according to species, in three somewhat variable genera. These are *Parvitermes*, *Tumulitermes* (fig. 4, K) and *Obtusitermes*, of which *Parvitermes* is probably slightly more primitive than the other two. The most specialised member of this secondary branch is *Trinervitermes*, in which the mandibles are reduced to simple lobes.

The tropicopolitan genus *Nasutitermes* (fig. 4, H, I, J.) includes species which show all the stages of the reduction of the points. Many Neotropical species have well developed points, and some have prominent marginal teeth. In contrast, a number of Australian species have lost the points altogether, and most of those from this region have weakly developed points. The Indo-Malayan and Ethiopian species are intermediate, rarely having any trace of marginal teeth. It is apparent that the genus *Nasutitermes* is a somewhat heterogeneous group of species which may require subdivision. At present it can only be represented on a hypothetical phylogenetic tree by a side branch, correct position of which is in some doubt.
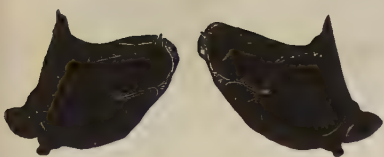
I. *Coarctotermes (C. coarctatus).*
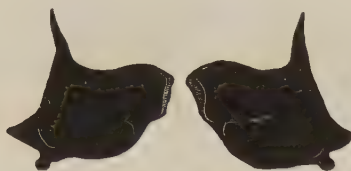
L. *Ceylonitermes.*
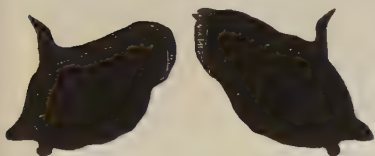
H. *tenuirostritermes.*
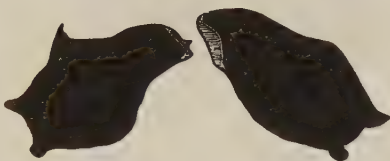
K. *Coarctotermes (C. tenebricus).*
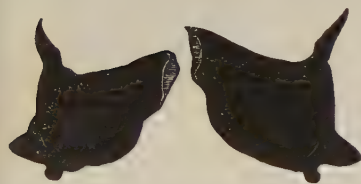
G. *Diversitermes.*
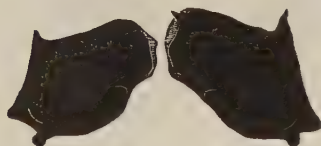
J. *Coarctotermes (C. clepsydra.)*

mitinae, *Procornitermes* branch.

The Paracornitemes branch.

The paucity of intermediate forms in the *Paracornitermes* branch makes the relationship of the genera somewhat obscure.   AHMAD classifies them into two categories: those which possess points, and those which do not. This is considered to be too arbitrary a division, and gives a rather mislead-ing picture of the probable evolution of the group.   It is apparent from the soldier caste that some species of *Eutermellus* are more primitive than was stated by AHMAD.   The soldier mandible of *E. bipartitus* (Sjöst) (5, G.) though much reduced in size, has a molar plate which bears better developed teeth and ridges than do those of most other nasute genera. The blade vestige is reduced to a tubercle, but the labrum apparently retains traces of the primitive trilobed shape seen in *Syntermes* and *Pro-cornitermes*.   The nose is markedly rugose, as in *Angularitermes*, and arises from the head capsule with abrupt change of contour at the base. The points are entirely lost in some species of *Eutermellus*, but most of the other features are retained.

C. *Lacessititermes.*
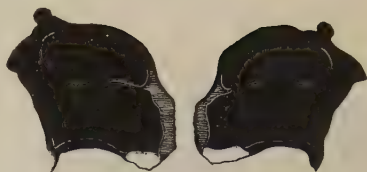
F. *Grallatotermes (G. africanus).*

B. *Hospitalitermes.*
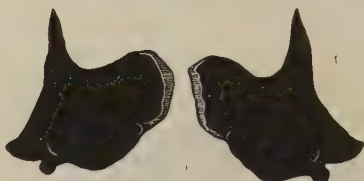
E. *Grallatotermes (G. admirabilis).*
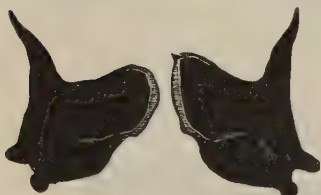
A. *Constrictotermes.*

D. *Bulbitermes.*

Fig. 4. — Soldier mandibles of the Nas

Another genus which in some species retains points on the soldier mandibles, is *Mimeutermes*, which is closely related to *Eutermellus*, but has evolved parallel to it, since both genera include species with and without points.

Mimeutermes is rather more specialised, particularly in the imago-worker mandibles, and the soldier labrum has lost all except slight traces of the trilobed structure. The points are well developed in *M. giffardii* Silv. (fig. 5, H.) somewhat reduced in *M. sorex* Silv. (fig. 5, H.) and absent in *M. edentatus* Sands (fig. 5, I.).

The blade vestiges are present and well developed in *Occasitermes* (fig. 5, J.) which represents another secondary branch, and which should probably also be separated from the branch which terminates in *Convexi-termes* (fig. 5, L.). This last is the most specialised genus, so far as soldier mandibles are concerned, in the whole *Paracornitermes* branch, having developed a thin patch of cuticle at the apex of the mandible similar to that in *Trinervitermes*.

The genus *Subulitermes* (fig. 5, K.) as constituted at present, apparently contains species related to each of the three secondary branches. If on further investigation this proves to be the case, the genus may require
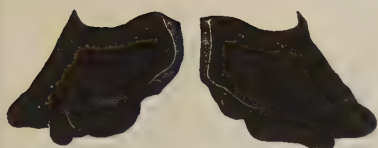
I. *Nasutitermes (N. kempæ)*.
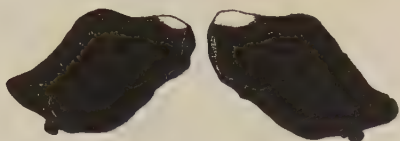
L. *Trinervitermes*.
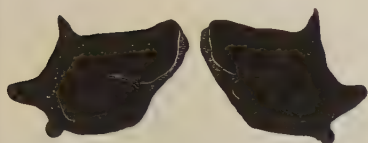
H. *Nasutitermes (N. usambarensis)*.
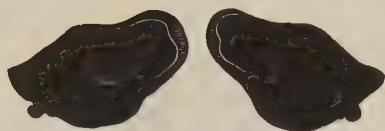
K. *Tumulitermes*.

G. *Havilanditermes*.

J. *Nasutitermes (N. anamalensis)*.

rmitinae, *Procornitermes* branch, continued.

subdivision, since any close resemblance between the present species would then be the result of convergent evolution.

Summary and Discussion.

Soldier mandibles representing 30 out of the 33 genera into which the subfamily Nasutitermitinae is divided have been studied and compared. All those described are illustrated, the most variable genera being represented by more than one species.

Though usually only of value as a generic character, the soldier mandibles are apparently specific in some genera (e. g. *Mimeutermes*). Conversely in the *Hospitalitermes-Grallatotermes* group of genera they are almost uniform.

The evidence of the soldier mandibles largely supports the phylogenetic conclusions which AHMAD offers in his work on the imago-worker mandibles. They indicate, however, a rather more frequent occurrence of parallel trends of evolution, and in some cases a slightly different relationship between genera.

C. *Armitermes (A festivellus)*

F. *Angularitermes.*

B. *Labiotermes.*

E. *Curvitermes* (after *Silvestri*, 1903).

A. *Paracornitermes.*

D. *Armitermes (A. chagresi).*
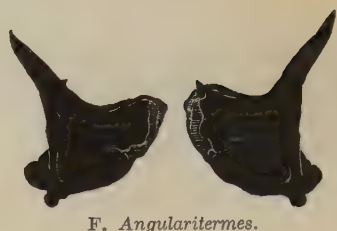
Fig. 5. — Soldier mandibles of the Nas

The two main branches of the subfamily, the *Procornitermes* branch and the *Paracornitermes* branch, are subdivided into a number of secondary branches. In the *Procornitermes* branch it is considered that *Longipeditermes* and *Hirtitermes* should occupy a more primitive position than that suggested by AHMAD. *Coarctotermes* is transferred from the "constricted-headed genera" to the *Velocitermes* branch in view of the presence of minute molar teeth on one or both soldier mandibles in all species, and the aberrant imago-worker mandible of *C. tenebricus* (Silv.), which is an indication of specialisation in this genus.

In the *Paracornitermes* branch three secondary branches are suggested, on morphological grounds. This division agrees with the zoogeographical distribution of the genera concerned, in the Neotropical, Ethiopian, and Australian regions.

I. *Mimeutermes (M. edentatus)*.
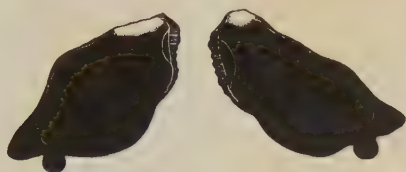
L. *Convexitermes*.
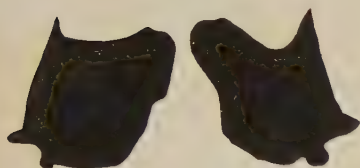
M. *sorex.*   M. *giffardii.*
H. *Mimeutermes* (after *Silvestri*, 1914).
* * * * *

K. *Subulitermes*.

G.*Eutermellus*.
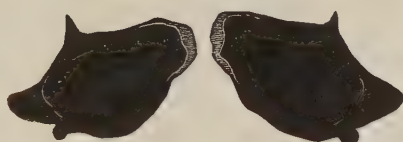
J. *Occasitermes*.
* * * * *

mitinae, *Paracornitermes* branch.

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INTERATTRACTION OLFACTIVE
CHEZ *CALOTERMES FLAVICOLLIS*
I. POUVOIR ATTRACTIF DES LARVES A L'ÉGARD DES DIFFÉRENTES CASTES

par

H. VERRON

(Laboratoire de l'Évolution des êtres organisés, Paris.)

On sait que l'interattraction joue un rôle très important dans les sociétés animales. Cette attraction mutuelle est de nature variée et peut dépendre soit de stimuli externes (stimuli olfactifs, visuels), soit de pulsions internes (appétition sociale de Wheeler). Chez les Termites, aucune étude de l'interattraction n'a été entreprise jusqu'ici de manière systématique.

J'ai donc essayé de mettre en évidence le rôle de l'olfaction dans l'attraction exercée par les larves de *Calotermes flavicollis* à l'égard des différents individus d'une colonie de la même espèce.

MATÉRIEL ET MÉTHODE

Toutes les expériences ont été faites en chambre noire, dans des conditions de température et d'hygrométrie rigoureusement contrôlées et aussi constantes que possible. Le choix d'une lumière rouge faible pour éclairer le dispositif expérimental nous a été suggéré par les travaux de RICHARD (1951).

Les insectes, pris dans un élevage au moment de l'utilisation, n'ont jamais été maintenus plus d'une heure en expérience et ont été remis immédiatement après usage dans leur colonie d'origine.

Pour étudier l'attraction olfactive, j'ai réalisé un olfactomètre (fig. 1) à l'aide d'une gouttière de verre de

Fig. 1.

30 cm de long sur 3 cm de diamètre, fermée dans sa longueur par une toile métallique très fine et bouchée aux extrémités par un tampon d'ouate. Cette gouttière, graduée en centimètres, est posée à l'envers sur six tubes équidistants de 9 cm de haut sur 2,5 cm de diamètre. Ces tubes sont emplis de sable humide jusqu'à 1,5 cm du bord.
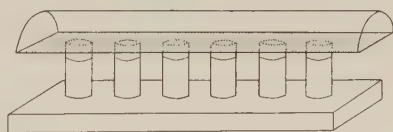
Le groupe attractif est mis dans un des tubes. Le sujet réacteur est déposé sur la toile métallique à une extrémité de la gouttière. Son comportement est observé pendant une heure, et sa position dans la gouttière est relevée toutes les trois minutes. On constate que l'animal parcourt plusieurs fois la longueur de la gouttière en marquant des arrêts plus ou moins prolongés au-dessus du tube où se trouve le groupe attractif. Le comportement est noté de la manière suivante : on considère dans la gouttière six zones égales correspondant à chacun des six tubes numérotés de 1 à 6. On porte sur un diagramme (fig. 2 et 3) la fréquence des passages de l'animal dans les différentes zones.

L'attraction est donc mesurée par le nombre d'arrêts que fait le sujet au-dessus de ses congénères.

Pour apprécier les mesures et voir si les résultats obtenus sont significativement différents de ceux qui seraient obtenus par un comportement au hasard de l'animal, on calcule le t de Student en appliquant la formule :

$$t = \frac{(m - \mu)}{\sigma/\sqrt{N}}$$

où m designe le nombre d'arrêts faits par le sujet au-dessus du groupe attractif ;

μ désigne le nombre d'arrêts correspondant au hasard ;

σ : la variance.

Pour éprouver la signification de la différence entre les résultats obtenus dans chaque série, on fait une analyse de la variance qui conduit à calculer le rapport de Snédécor donné par la formule :

$$F = \frac{Sng \, (mg - m)^2}{K - 1} \diagdown \frac{S\Sigma \, (x - mg)^2}{N - K}$$

dans laquelle :

ng désigne le nombre de valeurs et Sng leur somme ;

mg désigne la moyenne des ng valeurs ;

K désigne le nombre de groupes ;

N désigne l'effectif total.

Le résultat obtenu est comparé aux nombres donnés dans la table de Snédécor. Selon qu'il est inférieur, légèrement ou très supérieur, on dit que le résultat est non significatif, significatif ou très significatif.

RÉSULTATS

A. — Expériences préliminaires.

1. *Expérience avec l'appareil vide.*

Afin de s'assurer de l'isotropie de l'appareil, une série de 20 expériences a été faite avec 20 sujets réacteurs différents sans groupe attractif. On constate (fig. 2) que l'animal ne marque aucune préférence pour un endroit

particulier de l'appareil, à l'exception des extrémités fermées par le tampon d'ouate. Le Termite s'attarde en effet sur le bouchon de coton par thigmo-tactisme.

2. *Mise en évidence d'une attraction d'ordre chimique.*

Dix expériences ont été réalisées pour montrer que l'attraction exercée sur le sujet réacteur est d'ordre chimique.

On dépose 40 cadavres de Termites dans un tube au centre de l'appareil. On remarque que l'animal s'arrête fréquemment au-dessus du tube contenant les cadavres. Ces expériences prouvent que le sujet est attiré par l'odeur de ses congé-nères.
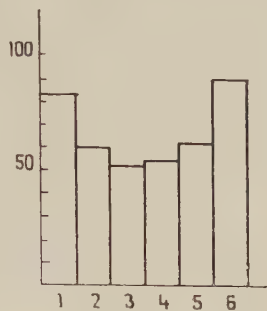
Fig. 2. — *Expérience avec l'appareil vide.*

En abscisse : les diffé-rentes zones de l'appareil numérotées de 1 à 6.

En ordonnée : le nombre d'arrêts effectués par l'ani-mal au-dessus de chaque tube.

B. — Étude de l'attraction olfactive.

Dans toutes les expériences qui vont suivre, le groupe attractif est uniquement composé de larves. Il s'agit de voir comment s'exerce l'attrac-tion olfactive en fonction de la caste et de la densité de groupement.

En ce qui concerne les castes : 4 types différents d'individus ont été uti-lisés : des larves, des nymphes, des soldats, des néoténiques.

De même, les expériences portent sur 4 densités différentes de groupe-ment : 5, 10, 15 et 20 sujets.

Pour chaque densité de groupement et pour chaque caste, 20 expériences
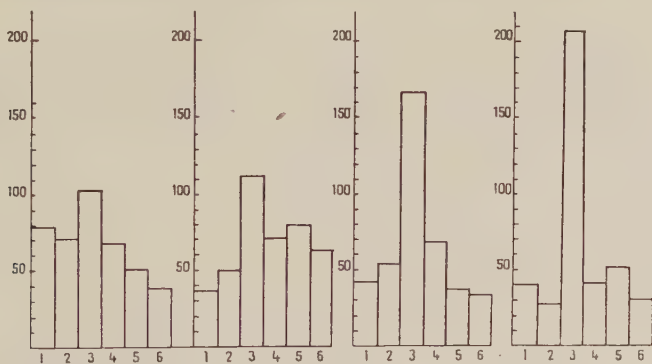
Fig. 3. — *Nymphes du septième stade.*

En abscisse : les différentes zones de l'appareil numérotées de 1 à 6.
En ordonnée : le nombre de passages effectués par l'animal au-dessous de chaque tube.
Au n° 3 : tube contenant le groupe stimulus.

ont été faites (soit au total 400 expériences) en changeant de sujet réacteur à chaque fois.

1. *Le sujet réacteur est une larve.* — On sait la difficulté qu'on éprouve à

déterminer de façon précise les différents stades larvaires. Les individus utilisés ici sont des larves de grande taille ne présentant pas d'ébauches alaires. Il s'agit donc soit de larves âgées (5e stade), soit de pseudergates. Les 100 expériences réalisées avec les larves sont réparties en séries de 20. Chaque série correspond à l'une des densités de groupement suivantes : 1, 5, 10, 15, 20 Termites. Les résultats (tableau I) montrent que l'attraction augmente avec la densité de groupement. On remarque toutefois qu'il n'y a pas de discrimination entre les densités 10 et 15.

L'analyse de la variance donne F = 7,64. Ce résultat très significatif montre qu'il y a un rapport très étroit entre l'attraction et la densité du groupement.
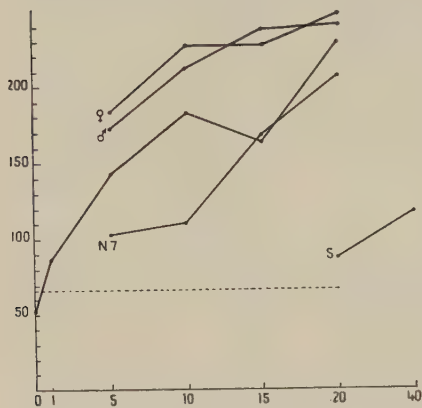
Fig. 4. — *Comparaisons intercastes.*

En abscisse : densité de groupement.
En ordonnée : nombre d'arrêts au-dessus du groupe stimulus.

2. *Le sujet réacteur est une nymphe du 7e stade* (fig. 3). — Ce stade étant facile à déterminer, on opère donc avec un matériel plus homogène, ce qui entraîne une plus grande régularité des résultats (tableau I). On remarque ici que la réactivité est à peu près la même pour les densités 5 et 10 et que le seuil d'excitation semble plus élevé que pour les larves puisque, pour une stimulation identique, les réponses sont beaucoup plus faibles.

L'analyse de la variance donne F = 6,87, qui est aussi un résultat très significatif.

3. *Le réacteur est un soldat.* — Pour des densités inférieures à 20, on n'obtient pas de réponses significatives. L'attraction n'est sensible qu'à partir d'un groupe stimulus de 20 sujets et n'augmente guère quand on double la population du groupe (tableau I). Le soldat semble moins sensible à l'odeur des larves que les représentants des autres castes.

Ceci est conforme à ce que l'on sait des soldats, qui, chez les Termites, ont un comportement très particulier.

Pour la densité de 20, le *t* de Student est tout juste significatif au seuil de P = 02.

4. *Le réacteur est un néoténique :* les résultats montrent qu'il n'y a pas de différence significative entre mâles et femelles. La comparaison avec les autres castes indique que les néoténiques sont très sensibles à l'odeur des larves. Ils donnent en effet les résultats les plus élevés. Par contre, ils semblent beaucoup moins sensibles aux différences de densités.

RÉSUMÉ

L'olfaction intervient dans l'interattraction entre les différents individus dans les colonies de *Calotermes flavicollis*.

Les larves sont très sensibles à l'odeur de leurs congénères et à la densité de groupement.

Les nymphes du 7e stade ont un seuil de sensibilité plus élevé et sont surtout sensibles à une densité de 15 ou 20 sujets.

Les néoténiques sont les plus sensibles à l'odeur des larves, mais ils réagissent moins aux différences de densité. Il ne semble pas y avoir de différence de sensibilité entre les sexes.

Les soldats sont les moins sensibles. Ils ne manifestent un intérêt pour les larves qu'à partir d'un groupement de 20 sujets.

TABLEAU I

	1	5	10	15	20	40
Larves	86	142	183	170	228	
Nymphes 7e		102	110	166	207	
Soldats					87	116
Néoténiques ♂		171	211	237	240	
Néoténiques ♀		184	228	227	249	

Summary.

Olfaction takes a part in the reciprocal attraction existing between the different individuals in the colonies of *Calotermes flavicollis*.

Larvæ are very responsive to the smell of other larvæ and to the density of grouping.

Nymphs of the 7th. instar exhibit a higher level of response and are especially sensitive to a grouping of 15 or 20 individuals.

Neotenics give the best response to the smell of larvæ, but do not react as well to the differences of density. There does not appear to be any difference in response between the sexes.

Soldiers are least sensitive ; they exhibit interest towards larvæ, but only for groups formed by 20 larvæ at least.

Zusammenfassung.

Der Geruchsinn spielt eine Rolle bei den gegenseitigen Beziehungen zwischen den verschiedenen Einzelwesen in den Kolonien von *Calotermes flavicollis*.

— Die Larven besitzen ein sehr feines Reaktionsvermögen auf den Geruch ihrer Artgenossen und die Dichte einer Gruppe.

— Die Nymphen des siebten Stadiums haben eine höhere Sensibilitätsschwelle und sprechen vor allem bei einer Gruppe von 15 oder 20 Wesen an.

— Die Neotenischen sind diejenigen, die am empfindlichsten auf den Geruch der Larven aussprechen.

Aber sie reagieren weniger auf die unterschiedliche Dichte.

Es gibt anscheinend keine unterschiedlichen Empfindungsfähigkeiten der Geschlechter.

— Die Soldaten sind diejenigen welche am wenigsten empfindungsfähig sind. Bei den Larven bringen sie erst einer Gruppe von 20 Wesen gegenüber Interesse entgegen.

L'IMPORTANCE DE L'APPROVISIONNEMENT EN EAU DANS LA RUCHE

par

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Au cours de recherches d'ordre pratique sur la possibilité de claustrer des ruches (1) nous avons été amenés à envisager particulièrement un point important : *l'apport d'eau à la ruche claustrée réduit, dans de fortes proportions, la mortalité des Abeilles.* Quel est son mode d'action dans ce phénomène ? C'est ce que nous allons essayer d'éclaircir dans cette note.

CHAUVIN (1952), étudiant la claustration des ruches, insiste sur le rôle que joue l'eau pendant cette opération. Certains apiculteurs claustrant leurs ruches au moment des traitements insecticides des colzas en fleurs versaient de l'eau directement sur les rayons à l'aide d'un arrosoir. Il s'ensuivait une mortalité ultérieure beaucoup moins forte. En effet, des Abeilles claustrées depuis plusieurs jours, à l'ouverture de la ruche, cherchent des points d'eau pour s'y abreuver longuement. Nous avons pensé que l'eau agissait soit en abreuvant les Abeilles, soit en provoquant, par son évaporation à l'intérieur de la ruche, un abaissement sensible de la température. D'après les observations que nous avons réalisées par la suite, il semble que les deux phénomènes interviennent.

Une note de LINDAUER (1955) parue ultérieurement à nos expériences nous a apporté des précisions à ce sujet. Étudiant « l'économie de l'eau et la régulation de la température d'une colonie d'Abeilles », il constate les faits suivants : quand la température menace de devenir excessive, les Abeilles se répartissent sur les rayons, ventilent et apportent de l'eau dans la ruche. L'eau est distribuée en petites quantités à l'intérieur des cellules et à l'extérieur, dans les dépressions situées entre les opercules. L'évaporation est accrue par la ventilation. Il s'ensuit un abaissement important de la température. Les Abeilles augmentent l'évaporation grâce à des mouvements constants de leur langue sous laquelle se maintient une goutte d'eau. Ces mouvements de la langue servent à la régulation thermique, mais aussi à concentrer le nectar.

L'eau n'est pas transportée par n'importe quelles Abeilles, mais par quelques-unes seulement, et distribuée dès leur retour à d'autres Abeilles qui en assurent la répartition à l'intérieur de la ruche. Il existe une relation directe entre l'élévation de température extérieure et l'activité des pour-

voyeuses d'eau, et les besoins en eau dépendent : 1º de l'importance du couvain non operculé ; d'après von RHEIN (1951), la teneur en eau de la nourriture du couvain est très forte ; pour les ouvrières, elle passe de 78,8 p. 100 le 1ᵉʳ jour à 54,6 p. 100 le 6ᵉ jour ; 2º de l'abondance de la miellée (le nectar peut contenir 70 p. 100 d'eau et plus, tandis que le miel n'en contient que 20 p. 100 ; 3º des conditions météorologiques : après une période de froid ou de pluie, les Abeilles n'ayant pu sortir, l'activité des pourvoyeuses en eau s'accroît fortement. On assiste à une véritable ruée vers les gouttes de rosée ou les sources d'eau. Les pourvoyeuses sortent à une température bien inférieure (6º) à celle exigée par les butineuses rapportant du pollen ou du nectar (10º et plus) suivant les colonies.

C'est ce qu'ont observé (nous l'avons vu également) les apiculteurs à la suite d'une claustration. Les Abeilles sortent peut-être pour s'abreuver, mais surtout pour chercher l'eau indispensable à l'élevage du couvain.

Ces observations sont en accord avec celles de CRANE : de petites colonies recevant de l'*eau pure* en nourrissement se développent aussi rapidement que celles nourries de sirop et plus rapidement que des colonies témoins non nourries.

Mais, avant de rapporter les faits que nous avons observés dans des ruches claustrées, ne pouvant par conséquent pas aller puiser d'eau au dehors et ne pouvant utiliser celle du nectar rapportée par les butineuses, il faut présenter quelques remarques sur la courbe thermique et sur la courbe de poids des ruches au cours d'une journée.

COURBE THERMIQUE ET COURBE DE POIDS D'UNE RUCHE NON CLAUSTRÉE (TÉMOIN) (Fig. 2, courbe nº 1.)

La courbe thermique était obtenue à l'aide de téléthermomètres enregistreurs, à sonde, placés, comme pour les expériences dont nous parlerons par la suite, dans une hausse et reposant sur les cadres du corps de ruche. La sonde se trouvait ainsi à quelques centimètres au-dessus du nid à couvain (position horizontale).

Pendant l'expérience, la température extérieure passa de 10-11º, le matin, à 19-21º, au cours de l'après-midi, où elle atteignit son maximum. Elle commençait à remonter le matin à partir de 8-9 heures suivant les jours.

La température à l'intérieur de la ruche témoin, non claustrée, variait très peu d'un jour à l'autre ; se situant vers 17-19º entre 5 heures et 6 heures du matin, elle montait régulièrement pour atteindre son maximum, 32-34º, à 15 heures et redescendait sans aucune irrégularité ; elle atteignait son minimum le lendemain matin à 5 heures environ.

Nous notons ici un décalage important dans les courbes ascendantes et non dans les descendantes. Le matin, alors que la température continue à décroître au dehors, dans la ruche elle *augmente sensiblement dès 5 heures*. Nous pensons qu'à partir de cette heure l'évaporation de l'eau du nectar est réduite et que le refroidissement supplémentaire qui en résulte a cessé

son effet. Cette hypothèse semble se confirmer d'après des courbes de poids de ruches placées en permanence sur des pèse-ruches enregistreurs, au cours d'une miellée importante. Sur des courbes de poids obtenues au laboratoire, nous remarquons que, chaque nuit, les balances accusent une perte de poids légère, mais régulière. Cette chute s'atténue ensuite et le poids se stabilise bien avant la reprise d'activité, tôt le matin. Cette reprise d'activité est caractérisée par une sortie en masse des butineuses, d'où la perte brutale de poids enregistrée. Juste avant cet accident de la courbe, nous notons le palier correspondant à la cessation de la ventilation et de l'évaporation de l'eau du nectar. Le soir, par contre, si la température décroît dans la ruche, en même temps et même un peu avant celle de l'extérieur, c'est à la suite de la reprise de ces phénomènes évaporatoires.

Cette théorie semble confirmée par les observations d'HAMBLETON (1925). Dans une étude approfondie des variations du poids des ruches, il constate qu'au cours d'une forte miellée (fig. 1) le nec-

Fig. 1. — Courbe d'évolution du poids d'une ruche au cours d'une journée pendant une forte miellée.

tar récolté en une journée est évaporé presque totalement au cours de la nuit suivante. De plus, cette évaporation amenant une perte de poids est liée à la température extérieure. Les Abeilles sont obligées de maintenir constante la température du nid à couvain ; aussi, par temps froid, l'évaporation est moins rapide ; les Abeilles évitent ainsi un refroidissement trop intense.

COURBE THERMIQUE D'UNE RUCHE CLAUSTRÉE SANS EAU
(Fig. 2, courbe n° 3.)

Le manque d'eau se fait légèrement sentir sur les maxima, qui sont supérieurs de 2° environ à ceux de la ruche témoin non claustrée, mais surtout sur les minima. L'évaporation du nectar étant nulle dans ce cas, la chute nocturne de température due à l'évaporation (démontrée par les variations de poids) est beaucoup plus lente et moins importante. Les minima se situent vers 23-24°, au lieu de 18° pour la ruche témoin ouverte.

L'EAU DANS LA RUCHE CLAUSTRÉE

Différentes techniques de claustration ont été utilisées. Au cours de nos expériences, nous avons utilisé des ruches Dadant 12 cadres, contenant 6, 7, 8 cadres de couvain operculé, du couvain non operculé et des populations semblables et fortes.

Nous rapportons dans le tableau suivant la mortalité observée au cours d'une première série d'expériences qui nous a permis de mettre au point un dispositif acceptable de claustration (n° 1 du tableau).

TABLEAU N° 1

SYSTÈME DE CLAUSTRATION.	MORTALITÉ (en vol. d'Abeilles mortes).	
	Avec eau (cm³).	Sans eau (cm³).
(1) Hausses grillagées	100	2 500
(2) Toile ménageant un grand espace devant le trou de vol (40 × 15 × 45).	2 000	4 000
(3) Toile ménageant un petit espace devant le trou de vol (20 × 15 × 45).	975	4 000

Ces résultats permettent d'affirmer que la présence d'eau dans les ruches, quel que soit le système de claustration utilisé, aide considérablement les Abeilles à supporter des températures extérieures élevées.

Ayant mis sommairement en évidence le rôle important de l'eau dans la ruche claustrée, nous avons repris son étude en l'administrant non plus dans un cadre-nourrisseur, mais directement à l'aide d'un arrosoir sur les cadres de la ruche, à différentes heures de la journée. Nous avons retenu ici un seul mode de claustration : celui qui nous a donné la mortalité moindre au cours de nos premiers essais.

L'HEURE D'APPROVISIONNEMENT EN EAU ET SES RÉPERCUSSIONS A L'INTÉRIEUR DE LA RUCHE

Les expériences ont été répétées deux fois pour les différents cas étudiés. Une ruche sur les deux a été ouverte après 5 jours, l'autre après 8 jours. Nous avons distribué l'eau tous les jours aux heures suivantes :

1er cas : 0,5 l à 7 heures.
2e — 2 fois 0,5 l à 11 heures et 15 heures.
3e — 0,5 l à 12 heures.
4e — 0,5 l à 19 heures.
5e — Eau dans cadre nourrisseur.
6e — 0,5 l sirop à 7 heures et 12 heures.

TABLEAU Nº 2

Nº	Heure de l'approvision-nement en eau.	Nombre de cadres de couvain.	Mortalité après 3 jours.	Mortalité après 5 jours.	Mortalité après 8 jours.	Mortalité totale.		Poids.			
						5 jours de claustra-tion.	8 jours de claustra-tion.	6-4	10-4	14-4	20-4
1	7 h.	6	350	150 ouverte		500		44,6	43	43,3	45,4
2	—	8	300	275	400		975	39,7	39	37,2	40,1
3	7 h. et 12 h. Sirop sucre.	8	375	100 ouverte		475		44,1	43,4	40,5	40,3
4	—	7	125	25	125		275	37,6	36,5	36,6	36,8
5	11 h. et 15 h.	6	375	175 ouverte		550		43,7	43,4	43	45,4
6	—	7	200	150	250		600	48	46,6	44,1	47,6
7	12 h.	6	125	125 ouverte		250		41,6	40	40,7	41,9
8	—	8	300	80	200		580	50,9	48,3	46,4	47,8
9	19 h.	6	500	125 ouverte		625		39,1	37,5	39,2	41,9
10	—	7	325	175	250		750	39,7	38,4	37,0	39,1
11	Eau dans cadre nourrisseur.	6	375	275 ouverte		650		42	40,4	41,9	44,7
12	—	6	175	125	325		625	42,6	41,7	39	40,7
13	Témoin 1.							53,9	58,7	60,9	64,6
14	Témoin 2.							49,6	52,7	53,9	56,8

Pendant la claustration, les ruches ont été pesées deux fois par jour, à 7 heures et à 19 heures, et une fois 6 jours après leur ouverture. Nous figurons dans le tableau n° 2 la mortalité observée dans tous les cas et l'évolution des poids des ruches au cours de l'expérience. Le 6-4 correspond au premier jour de claustration, le 10-4 à la fin de la claustration de la moitié des ruches, le 144, celle de la seconde moitié. Dans aucun cas, même après 8 jours de claustration, la mortalité n'est excessive, contrairement à ce que nous avons observé en l'absence d'eau. Le rucher, abrité du vent, se trouvait dans une zone où la température était de beaucoup supérieure à celle enregistrée à l'ombre au même moment. Les pertes de poids ne sont jamais importantes, et, dès l'ouverture, les ruches reprennent une activité normale comme les résultats des pesées faites 6 jours après nous le prouvent. Seule la ruche n° 3 a perdu aussitôt 3 kg : ceci n'est pas dû à la claustration, mais seulement à un changement de place fait par erreur au cours d'une pesée. Toutes les ruches, à l'ouverture, étaient dans un état normal. L'élevage du couvain a continué, ainsi que la ponte, tandis que, dans les ruches claustrées sans eau, au cours de la première série d'expériences, *la reine avait cessé de pondre*. Les pertes de poids enregistrées sont faibles. La consommation de miel n'a donc pas été excessive.

A. — ACTION SUR LA TEMPÉRATURE

L'heure de l'apport d'eau a la plus grande influence sur la température à l'intérieur de la ruche.

APPORT D'EAU A 12 HEURES
(Fig. 2.)

Un apport à midi, soit deux heures environ avant que la température atteigne à l'extérieur son maximum, maintient celle-ci au-dessous de 25°; son action se fait sentir d'une façon durable. Si nous considérons la courbe de température d'une journée complète, nous observons les faits suivants : dès 7 heures du matin (fragment A-B), léger réchauffement ; la température passe de 20-22° à 22-23°. C'est alors que nous versons l'eau dans la ruche (point B). Il s'ensuit un refroidissement brusque jusqu'à ce que soit atteinte une température voisine de la température extérieure (16-18°). VERRON (1955) avait remarqué, au cours d'expériences antérieures, qu'à la suite de pulvérisations d'eau à l'intérieur d'une ruche les Abeilles réagissaient immédiatement par un bruissement correspondant à une ventilation importante. Cette ventilation évapore l'eau en même temps qu'elle refroidit la ruche. C'est ce qui explique la suite de la courbe. La température dans la ruche se maintient au-dessous de la température extérieure, sauf vers 16 heures (point C), où, tous les jours, nous notons une légère remontée, 5-6° (C-D), pour atteindre 19-22°, soit la même température que le matin à 7 heures (point A). Après cette remontée, nous assis-

tons à une nouvelle chute brusque (D-E) qui aboutit, vers 19 heures, à une température nettement inférieure à la température extérieure (point E, 12-14⁰ au lieu de 15-18⁰). Au même moment, la température à l'intérieur de la ruche témoin lui est supérieure de plus de 10⁰. Dès que la température accuse une baisse, les Abeilles cessent de ventiler, et la température monte en flèche (segment E-F) pour se stabiliser vers 22-24⁰ et y demeurer toute la nuit (segment F-A). Nous atteignons à ce moment (segment F-B), dans la ruche claustrée, la température maximum, tandis qu'au dehors et dans la ruche témoin elle est à son minimum. Ceci s'explique par ce que nous avons dit auparavant au sujet de l'évaporation de l'eau du nectar. Ces observations nous obligent à admettre qu'il reste encore de l'eau à évaporer
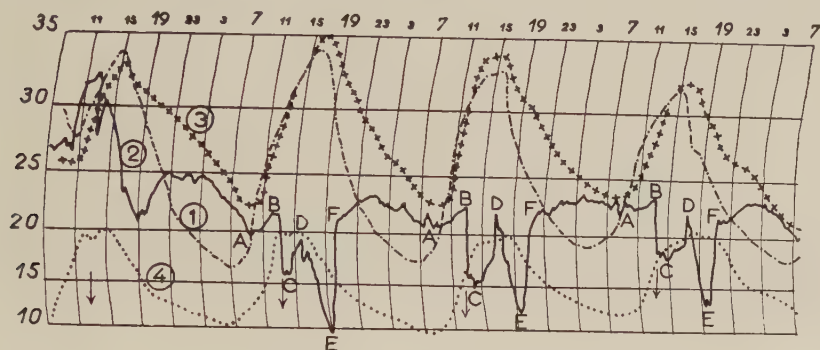
Fig. 2. — Courbes de température :

N⁰ 1, dans une ruche non claustrée.
N⁰ 2, dans une ruche claustrée abreuvée à 12 heures.
N⁰ 3, dans une ruche claustrée non abreuvée.
N⁰ 4, température extérieure à l'ombre.

le lendemain matin, sinon la courbe de température devrait coïncider avec celle de la ruche témoin, alors qu'elle se situe en dessous. LINDAUER a d'ailleurs observé, nous l'avons vu, un emmagasinement de l'eau à l'intérieur et à l'extérieur des cellules. Cette inversion de la courbe des températures montre que les Abeilles luttent, grâce à l'eau qu'elles évaporent, davantage contre une température excessive que contre l'élévation de température en soi. Ces faits sont en rapport avec les observations de LINDAUER : la sortie des pourvoyeuses en eau est étroitement liée aux variations de température, *surtout au-dessus d'un seuil dépassant 25⁰.*

DOUBLE APPORT D'EAU A 11 HEURES ET 15 HEURES
(Fig. 3.)

Les différences entre les deux courbes sont dues à l'apport d'eau supplémentaire à 15 heures. Son action est importante et tend à maintenir la température assez voisine de la température extérieure. La basse température s'explique par un excès permanent d'eau dans la ruche. Les Abeilles ventilent sans cesse et font baisser la température à un degré tel qu'à lon-

gue échéance elle risque de nuire à la colonie. Puisque la mortalité au
bout de 8 jours est semblable à celle observée dans les autres cas, on peut
penser toutefois que les Abeilles adultes ne souffrent pas trop de cette basse
température. La température *à l'intérieur du nid à couvain*, d'ailleurs, est
maintenue voisine de 35⁰ pendant les 8 jours de claustration grâce à un gros
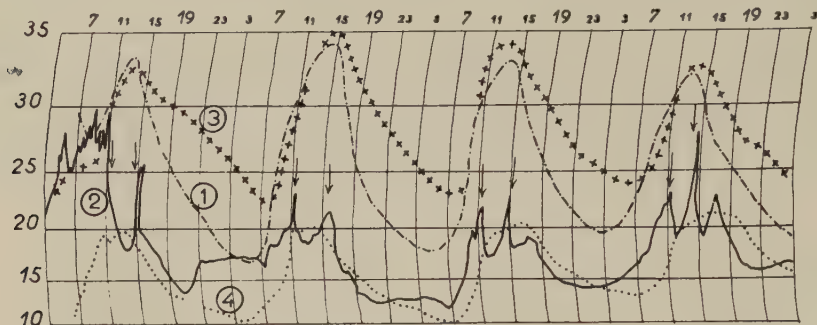
Fig. 3. — Eau à 11 heures et 15 heures (courbe n⁰ 2).

travail de régulation thermique, et à l'ouverture de la ruche le couvain
semble normal. Cet effort demandé aux Abeilles pourrait-il durer plus long-
temps ? Nos données ne nous permettent pas de répondre actuellement.

APPORT D'EAU A 7 HEURES
(Fig. 4.)

Il a peu d'effet à l'intérieur de la ruche, comme en témoigne la courbe de
température. Les maxima se situent toutefois vers 28-32⁰, au lieu de
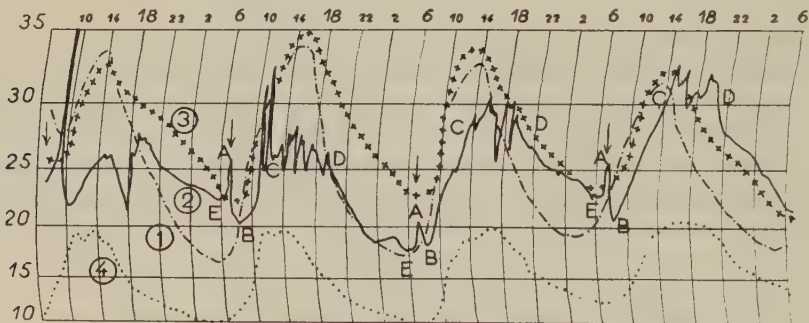
Fig. 4. — Eau à 7 heures (courbe n⁰ 2).

33-34⁰ pour la ruche témoin, avec variations parallèles à l'intérieur et à
l'extérieur. Au moment de l'apport d'eau (Point A), on note un abaissement
brusque de la température (A-B), succédant à une légère hausse (segment
E-A), qui retarde le réchauffement matinal de chaque jour. Nous pensons

que toute l'eau a été utilisée ou éliminée rapidement. Toute l'eau ayant dis-
paru il s'ensuit une élévation rapide, non freinée, de la température à
l'intérieur de la ruche, au cours de la journée (B-C). Nous avons vu que, la
nuit, la ruche témoin ouverte est refroidie par l'évaporation de l'eau du
nectar rapporté par les butineuses au cours de la journée.

La ruche claustrée sans eau se refroidit moins et moins vite que la ruche
ouverte. Il en est de même de la ruche claustrée approvisionnée en eau à
7 heures du matin. Les courbes de température dans ces deux derniers
cas coïncident à peu près (segment D-E). Ceci permet d'affirmer qu'il ne
reste plus de traces d'eau dans la ruche et confirme notre hypothèse de son
élimination rapide au début de la matinée.

DOUBLE APPORT DE SIROP DE SUCRE A 7 HEURES ET 12 HEURES
(Fig. 5.)

Le sirop de sucre (1 kg de sucre pour 1 l d'eau) donné en deux fois,
à 7 heures et à 12 heures, a pour effet de maintenir la température à l'inté-
rieur de la ruche au-dessous de 30⁰. Les minima coïncident avec ceux de
la ruche témoin. La distribution de midi tend à faire baisser sensiblement la
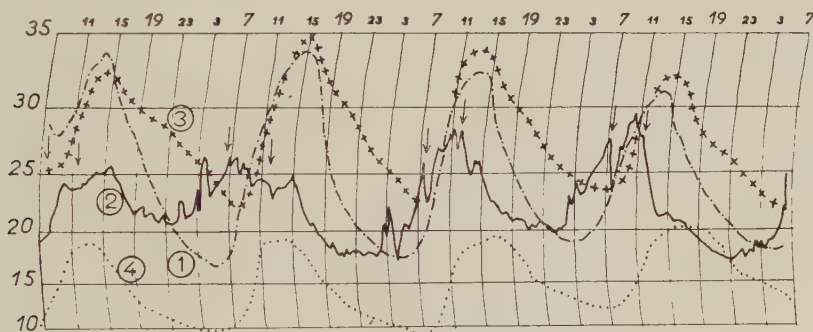
Fig. 5. — Sirop de sucre à 7 heures et 12 heures (courbe n⁰ 2).

température, qui atteindrait justement son maximum à ce moment. Comme
dans le cas de l'eau pure apportée à 7 heures, le premier approvisionnement
n'a pas de répercussions importantes. A 12 heures, la température est
voisine de celle de la ruche témoin. Contrairement à ce que nous observions
dans le cas d'un seul apport d'eau fait à midi, nous ne voyons pas ici de
minima très bas. La température ne descend pas au-dessous de 17-18⁰. Le
sucre serait consommé tout de suite, au moment où le sirop est versé
sur les cadres. Cette consommation de sucre apporterait assez de calories
pour expliquer cette différence.

Remarque: les différences brusques de température observées parfois
(fig. 4), pouvant atteindre 10⁰, sont dues à une obstruction du trou de
vol par les Abeilles, qui arrivent à occuper tout l'espace libre réservé pour

l'aération devant l'entrée de la ruche. L'affluence dans cette zone ne dure
jamais longtemps, et la température baisse aussi vite qu'elle est montée.

B. — *ACTION SUR LA MORTALITÉ*

Les mortalités les plus fortes surviennent dans les ruches où la tempé-
rature monte le plus (apport à 7 heures du matin). Nous ne disposions pas
de sondes en nombre suffisant au moment de l'expérience et nous n'avons
pas la courbe de température correspondant à l'approvisionnement en eau
à 19 heures. La mortalité y est importante, et on a le droit de supposer que
l'eau apportée à cette heure-là, plus encore que celle apportée à 7 heures du
matin, se trouve totalement bue ou évaporée avant que, le lendemain, la
température extérieure atteigne son maximum. Comme l'eau contenue
dans le nectar, elle doit être évaporée totalement au cours de la nuit.

Nous sommes en présence ici d'un phénomène biologique bien connu :
un approvisionnement suffisant en eau augmente considérablement la
résistance à la chaleur. Il est probable en effet que les Abeilles utilisent cette
eau pour nourrir le couvain, mais qu'elles s'en servent également pour leur
besoin propre.

Remarque : nous avons compté 400 Abeilles dans 100 cm³. Une reine pond
en moyenne 1 200 œufs par jour (ce chiffre étant très variable suivant les
reines et pouvant dépasser 4 000). Il naît et il meurt donc dans une ruche,
environ 300 cm³ d'Abeilles, en admettant qu'elles vivent toutes sensible-
ment aussi longtemps. Ces Abeilles meurent sans que l'apiculteur s'en rende
compte, le plus souvent au cours d'un butinage.

Pendant les 4 jours, 5 jours et 8 jours de claustration, il meurt donc nor-
malement 1 200 cm³ soit 4 800 Abeilles, 1 500 cm³ soit 6 000 Abeilles,
2 400 cm³ soit 9 600 Abeilles, chiffres toujours supérieurs à ceux obtenus
dans nos ruches claustrées approvisionnées en eau. On peut donc considérer
que la mortalité observée dans les ruches claustrées est normale, sans plus.
Le supplément qui meurt quand la ruche est ouverte est dû à la fatigue
qui épuise plus rapidement les Abeilles et réduit d'autant la durée de leur
vie.

C. — *ACTION SUR LE POIDS DE LA RUCHE*

Les pertes de poids enregistrées au cours de la claustration semblent peu
affectées quelle que soit l'heure de l'approvisionnement. Seul le sirop de
sucre nous donne un résultat intéressant que nous venons de signaler : la
perte de poids (ruche n⁰ 4) n'est alors que de 1 kg après 8 jours de claus-
tration (l'apport de sucre, pendant cette période, a été d'environ 4 kg), tandis
qu'avec l'eau, pour des ruches ayant un poids initial voisin, au bout du
même temps, elle atteint 2,5 kg (ruche n⁰ 2, approvisionnée en eau à 7 heures),
2,7 kg (ruche n⁰ 10, approvisionnée en eau à 19 heures), 3,6 kg (ruche n⁰ 12
alimentée en eau au moyen d'un cadre nourrisseur), et, pour des ruches plus

lourdes au moment de la claustration, elle dépasse 4 kg (ruche n° 8, approvisionnée en eau à midi). Sans pouvoir l'affirmer, il est logique de penser que le miel non operculé a été consommé en premier.

CONCLUSION

1° La montée thermique après la claustration semble provenir de l'agitation des butineuses.

2° Mais cette agitation semble due uniquement au besoin d'eau.

3° *Les besoins d'eau sont considérables, surtout quand la température s'élève.* La teneur en eau de la nourriture des larves dépasse 50 p. 100, tandis que le miel n'en contient que 20 p. 100. De plus, des Abeilles non abreuvées ne survivent pas à l'étuve à 30° au-delà de 48 heures. Weippl (8) évalue à 20 kg les besoins en eau pure, sans compter celle tirée du nectar, pour une forte population au cours d'une année (20 p. 100 environ de la nourriture totale). Il semble qu'il s'agisse ici de l'eau consommée et non de l'eau servant par son évaporation à la régulation thermique de la ruche quand la température intérieure menace de devenir excessive. Mais nos recherches ne nous permettent pas de mesurer l'importance relative de l'eau de consommation et de l'eau « de refroidissement ».

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THE FORAGING BEHAVIOR OF HONEYBEES
ON HAIRY VETCH
II. THE FORAGING AREA AND FORAGING SPEED (1)

by

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Honeybees foraging from blossoms of most plant species are rather similar in their methods of work, and careful observations are necessary to discern minor individual differences. Under these circumstances the student of foraging behavior must guard against the unconscious assumption that any one individual is representative of the entire population. This is not true, however, of the student of bees working hairy vetch. The bees differ so widely from one another in their methods and approach to foraging that the individuality of the bees is a most obvious and striking phenomenon, and the student must guard against the anthropomorphic assumptions that could easily follow from ascribing too much individuality to bees.

MATERIALS AND METHODS

In 1953, 1954, and 1955 studies were conducted on the behavior of honeybees (*Apis mellifera* L.) foraging from hairy vetch (*Vicia villosa* Roth.). The technique used in determining the nectar flow, nectar concentration, amount of bloom, and population of foragers have been published

Fig. 1. — Frequency distributions of the estimated distances between successive racemes of hairy vetch visited by tripping and base working honeybees.

(WEAVER, 1956 *a*, 1956 *b*). Most of the detailed studies of foraging behavior were conducted in the same field throughout any one year; this is designated below as the experimental field.

A few bees were marked by RIBBAND'S (1949) technique for repeated observations, but virtually all of the quantitative data were taken on bees found at random in the field, and presumably most of the bees were observed only once..

The length of time bees spent in tripping blossoms and the total time required to forage from them was measured with a stop watch in 1955. The time required to
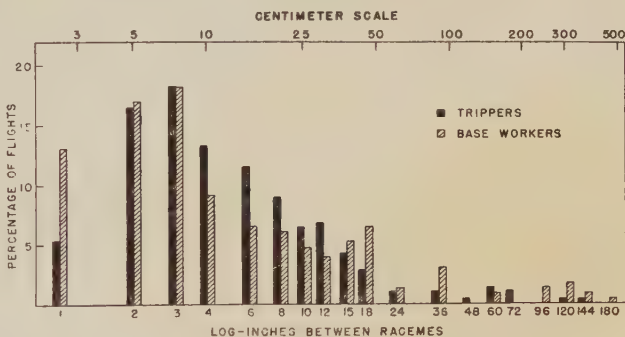
trip a blossom was measured to the nearest 0.1 second from the time the tongue was inserted into the mouth of the blossom until the keel was thrust downward completely free of the sexual column.   The time required to forage from a blossom, or the time spent in unsuccessfully attempting to forage, was measured to the nearest second as the time elapsed from the first attempt to insert the tongue into the blossom until the tongue was withdrawn.   Data on the time required to forage blossoms that obviously had been tripped previously were recorded separately.   For some of these measurement, the first bee that came into view in an area was timed while visiting one, or each of a very few blossoms, her foraging method and the forage she gathered were recorded, and then the observer moved three paces and collected data on the first bee that came into view at the new location.   Other bees were timed during visits to many successive blossoms.   The analyses of variance which were used in the statistical treatment of these data follow the methods given by SNEDECOR (1946).   Only the mean and its standard error were calculated for some of the data.

The over-all foraging speed of bees was determined by counting the number of blossoms foraged over a measured period of time by randomly selected individual bees. In 1953 only the successfully foraged blossoms and their racemes were counted.   In 1954 and 1955 the number of blossoms which a bee made a definite unsuccessful attempt to work were recorded separately from the successfully visited blossoms. Hand tally registers were used in keeping the counts.   The length of time over which the counts were made was taken with a stop watch and rounded to the nearest 0.1 minute.   Data on bees observed for less than 1.5 minutes were discarded.   All of this information plus the time of the observation, the forage gathered, the observed foraging area, the general foraging behavior, and the pecularities of behavior of each bee were recorded.

RESULTS AND DISCUSSION

In a previous communication (WEAVER, 1956 *b*) it was pointed out that the honeybee can reach the nectar from the mouth of the hairy vetch blossom by tripping it, or she can insert her tongue between the petals at the base of the corolla tube and reach the nectar.   These non-tripping bees are called base workers, and they gather nectar only.   The trippers forage in the mouth of the blossom for pollen only, or they insert the tongue into the blossom to their right or to their left of the sexual column and forage for nectar only or for both nectar and pollen.   The number of foragers of each type is variable and some of the variability can be related to the nectar flow.   The present communication reports studies of other aspects of foraging behavior.

Foraging Areas. — During the first few hours after colonies began to forage from vetch for the first time, there were always many more foragers near the colonies than farther away.   While bees were learning to forage from vetch blossoms they were very nervous and often flew great distances. It is believed that this helped to spread the foragers rather evenly over the field, and that the foraging area may have become fairly well fixed in the locality where the bee finished gathering the first load after the foraging method was learned.   Attempts to study the problem by marking bees that were learning to forage were unsuccessful; none of these bees were ever seen again, and it is not known that any of them resumed foraging.

Marked bees with an established foraging method could be found repeatedly, though with some difficulty. These bees were followed during several foraging expeditions to confirm the findings of RIBBANDS (1949) and SINGH (1950) that bees return to the same region on successive trips to the field and forage repeatedly over the same rather ill-defined area. These observations were made near landmarks of various kinds which could have served to orient the foragers, so it is not known how accurately a bee could determine a previous foraging area at a considerable distance from any landmarks other than the vetch itself. Since the vetch vines grow upward in clumps at various places with the surrounding vines being more reclinate, the topography of the field may help to delineate the foraging areas. Bees often foraged from a long narrow area along the side of a road, and it appeared that during a good nectar flow one marked bee foraged an oblong area which followed a series of clumps in the vetch.

When her load was almost complete a bee always visited several blossoms which she made little or no attempt to trip; these appeared to be exploratory visits. The return to the hive usually followed immediately after a number of these visits, though occasionally the bee successfully foraged from one or two blossoms just before leaving the field. During a good nectar flow the explored racemes were always close together, and the bee circled the area before returning to the hive. Presumably the forager was orienting herself for a return visit to the field and was establishing the direction of the colony. During a poor flow the exploratory visits might be scattered over a wide area, and bees sometimes lefts the field without circling. In these cases the bee flew upward for less than a meter before turning toward the apiary; the approximate direction of the colony would have to be known before flight became level.

RIBBANDS (1949, 1953) emphasized the comparisons which foraging bees continuously make between present yields from blossoms and the memory of past yields. Opportunity for such comparisons between the plants of one species over a short period of time and in a narrow area in the field often can be seen. It was not uncommon for a bee to forage for an extended time in an area much less than a square meter in size, fly three or more meters, and work quickly back to the original area, foraging one or two blossoms on each of several racemes between the two locations. Presumably the yields from the explored areas were not sufficiently better than the yields in the original area to cause the bee to change foraging localities. Often a bee would make several successive long flights with only perfunctor efforts to trip most blossoms, as if dissatisfied with the yields everywhere. One bee that made a definite effort to gather both pollen and nectar from most vetch blossoms alighted on a flower of the sensitive briar, *Neptunia* sp., ran over the anthers, and immediately returned to foraging vetch. Other bees had already gathered the pollen from this and the surrounding *Neptunia* blossoms. Such observations may have been more common if there had been more competing blossoms of different species.

Foragers also compare the yields of nectar on successive days. When,

the nectar flow deteriorated, bees foraged and explored over wider areas, flew great distances more often, spent more time exploring, and were less persistent in their efforts to trip many of the blossoms than when the nectar flow was constantly poor or was improving. Differences in the manner of work were so marked that from observations on foraging behavior alone, the gain in weight of a colony of bees as compared to the gain on the preceding day could be accurately predicted. The over-all impressions of foraging behavior were much more useful and accurate than the quantitative data for making predictions. Measurements of the amount of nectar in blossoms in 1955 indicated that the differences in foraging behavior in that year were caused by the amount of nectar available and not by the direct effects of the weather on the bees.

In addition to the elasticity of the foraging area which may cause a bee to discover more attractive vetch at a considerable distance from the point at which she started foraging, bees sometimes change to a foraging area completely removed from the old one. In 1954 the experimental field was among the first in the region to come into bloom, and there was a mean 2.2 foraging bees per square meter of vetch during the first ten days of heavy bloom. The nectar flow was slow, and following several days of inclement weather that reduced the foraging population, the number of foragers in the experimental field fell and remained near 1.1 bees per square meter for the rest of the season. In 1955 the experimental field was among the last to come into bloom, and although there was an apiary in the field there were few bees working the vetch until and an additional colony was brought into the field after the vetch was virtually in full bloom. During the next week there were 0.6 bees per square meter of vetch. The experimental field had more nectar per blossom and nectar of a higher sugar content than at least one nearby field that had come into bloom earlier and had more foragers. During three days of cloudy weather with intermittent showers the foraging population rose sharply and averaged 2.7 bees per square meter during the remainder of the blooming period, with means of more than 4 bees per square meter being common during periods of maximum foraging activity. Both the interruption of foraging and the threat of rain that made it dangerous for the bees to go far from the hive, as well as the greater attractiveness of the vetch in the experimental field, may have made it easier for scout bees to recruit foragers to the new area.

Aggressive Behavior. Competition from other foragers is important in determining the size of the foraging area. This competition may operate by decreasing the amount of nectar available from the blossoms or by the reaction of a bee to the physical presence of competing foragers. Often a bee was observed to collide with a nearby forager in a purposeful manner or to fly threateningly toward another bee without actually touching her. The agressor in each of these observations continued to forage nearby; the bee that was bumped or threatened sometimes flew several meters

and sometimes continued to forage nearby. When neither bee left the vicinity there was sometimes a prolonged struggle, with contact between the bees every time they were on the wing at the same time, and with one or the other of the bees sometimes being attacked while foraging from a blossom. Some of these bees were always passive but would refuse to leave the area; others would become aggressive on some of the flights so that occasionally both bees attacked the other at the same time. One bee was observed to collide with another forager that was flying past, and then to visit a raceme deep in encircling vines. The bee that was attacked had given no indication of stopping in the area, but she immediately whirled in pursuit of her attacker, bumping into several vines in the recklessness of her pursuit. One bee that was being kept under prolonged observation moved about 2 meters in one flight after being bumped, and then quickly foraged from several racemes on her way back to her original narrow area which she continued to work. Another bee that was under observation flew more than three meters to forage in a new area; soon after beginning to forage she was attacked by another bee already in the vicinity, and moved more than a meter before visiting another blossom; another bee was later observed to behave in the same manner. One bee flew about 3 meters from an area which she had been working for some time and bumped another forager before visiting a blossom at the new location. The bee that was attacked flew away, and the aggressor began to forage in the new area. This aggressive behavior by foraging bees is probably an aid in keeping a foraging area free of too much competition from other bees; and possibly aids bees in moving into new foraging areas. Interestingly, when the competition between foragers became intense and there were over 4 bees per square meter during periods of maximum foraging activity, this aggressive behavior virtually ceased, and bees paid little attention to nearby foragers.

Distance of Flights. It was difficult to keep base workers under observation because of their frequent long flights. The eyes and antennae of the base workers, unlike those of the trippers, were fully exposed while they foraged from blossoms, and the presence of an observer often seemed to disturb them and cause some of the longer flights. They also seemed to be more sensitive than trippers to the presence of competing foragers; base workers were more prone to take evasive action when another forager flew near by, and often moved to a blossom deep in encircling vines, or flew away from the area, after such evasive action. Records of the conditions surrounding over 100 randomly observed flights of more than a meter did not indicate clearly whether or not base workers normally move long distances more often than trippers. By recording only the estimated distance between successive racemes visited by a bee, it was possible for the observer to stay farther from each bee than was possible when the foraging behavior on individual blossoms was being recorded. Each day that this technique was used, base workers and trippers were

observed alternately for an approximately equal lenght of time in vetch with about 600 racemes per square meter. The nectar flow and concentration fluctuated rather widely during the days in 1954 when these observations were made, and the distances between racemes were determined on days when the nectar flow was equal to, better than, and poorer than on the preceding day.

Estimated distances in inches between racemes visited were recorded on 232 flights by 11 base workers, and on 277 flights by 10 tripping bees. The mean for the estimated distances was 23 cm. for trippers, and 32 cm. for base workers. Since the relatively rare longer flights unduely influence the mean, the frequency distributions of the estimated distance were determined. Figure 1 is a histogram of the percentage of flights plotted against the logarithmically spaced estimated inches between racemes. For ease of conversion, a centimeter scale is also given. It can be seen that base workers were more prone to move to contiguous racemes than trippers. They also sometimes crawled along the stem to racemes more than 5 cm. away; trippers usually flew, even in moving to contiguous racemes. The distribution curves for the two types of foragers are similar, though the differences at some of the shorter distances are greater than would be expected from sampling variation or errors in estimating distances. If the data are grouped so that there are four estimated distances in each of the first three groups, the percentage of flights that falls within each group is:

Estimated.		Percentage of Flights by :		
Inches.	Centimeters.	Trippers.	Base. Workers.	All. Bees.
0-5	0-13	53	57	55
5-13	13-33	34	22	28
13-42	33-105	9	16	13
42 <	105 <	4	5	4

Although the divisions between groups fall at points on the curve where maximum accuracy of estimate is expected, the distances obviously were not as precisely estimated as would be implied by the above group limits. These percentages, however, are not greatly affected by the errors in estimating distances that were most likely to have occurred. Thus, if we assume that half of the estimates of each distance were too low, and should been estimated as the next greater distance, the percentage in each group becomes, for trippers, 47, 37, 12 and 4, respectively. The assumption that half of the distances were underestimated, or that half of the distances were randomly mis-estimated to the same degree, results in smaller changes in the original percentages.

Foraging Speed. The foraging method of 300 bees and the time in seconds required for each bee, with few exceptions, to forage from one or

each of several blossoms was determined in 1955.   The data on successful visits to previously untripped blossoms were analyzed in an attempt to discover the sources of any nonrandom variation that might have occurred in foraging time.   Trippers working to the right and left of the sexual column did not differ significantly in foraging speed, so this classification

TABLE 1. — Mean time in seconds required by 50 honeybees to forage from vetch blossoms on each of 6 occasions in 1955.

Date.	Time Hr.	TRIPPERS.						BASE WORKERS.		ALL BEES.	
		Nectar only.		Nect. and Pol.		Pollen only.		No. Blos.	Sec./ Blos.	Total and Mean.	
		No. Blos.	Sec./ Blos.	No. Blos.	Sec./ Blos.	No. Blos.	Sec./ Blos.			No. Blos.	Sec./ Blos.
5/5	1100	31	9.0	36	9.4	0	—	3	10.0	70	9.3
5/5	1530	14	10.8	19	9.2	0	—	8	5.8	41	9.1
5/7	0830	23	11.5	19	9.9	2	4.5	5	6.8	49	10.2
5/7	1100	21	10.8	20	10.7	7	5.4	10	12.1	58	10.3
5/12	1300	15	11.8	30	10.3	4	3.7	9	11.1	58	10.4
5/17	1100	7	9.4	29	11.6	2	2.5	34	7.3	72	9.1
Total and Mean ...		111	10.5	153	10.2	15	4.4	69	8.5	348	9.7

is omitted from Table 1, which summarizes the data.   The time required to forage blossoms did not vary significantly between the different dates and hours on which observations were made.   The differences in mean foraging times of bees classified according to forage gathered were significant beyond the 0.01 level.   An examination of the data shows little difference between trippers foraging for nectar only and those gathering both nectar and pollen.   This is not surprising since few of the bees that gathered both pollen and nectar foraged specifically for pollen; rather they accumulated the pollen that accidentally clung to them.   The bees gathering pollen only and the base workers were strikingly different in foraging speed from these bees and from each other.   It took less time for a bee to forage a blossom for pollen than for nectar, but the time required by trippers and base workers to remove nectar was probably approximately equal.   Nine bees timed in tripping each of 60 blossoms required a mean of 2.7 ± 0.2 seconds to trip a blossom; no good data was obtained on the length of time required by base workers to insert the tongue into blossoms, but this certainly required less time than tripping.

Records were also made of the number of seconds required for individual bees gathering nectar only or both nectar and pollen to forage successfully from each for 10 or more blossoms.   These data are summarized in Table 2.

Because of the findings presented above the time at which the observations were made, the forage gathered, and the direction of entry into blossoms were disregarded and an analysis of variance was run to determine whether or not these twelve bees differed from each other in mean number of seconds required to forage from blossoms. The highly significant F value indicates that they did differ among themselves. The data on bees No. 7 and 8 were taken during a high wind, and these bees sometimes clung to a blossom for up to 46 seconds while the wind buffeted the raceme about. This seemingly accounts for the slow foraging speed of these bees, but if the data on bees 7 and 8 are discarded, the remaining bees differ significantly from each other.

The data on bees observed successfully foraging from less than 10 blossoms are combined and presented in Table 2 as miscellaneous bees. Included in this group are data on unsuccessful visits and visits to previous by tripped blossoms by bees whose successful visits are given in Table 1. Observations on the time required for several base workers to forage from blossoms are also grouped and presented in Table 2. The data on base workers in Tables 1 and 2 are not in very good agreement, but this seems to be due to sampling variation.

TABLE 2. — Mean time in seconds required by several bees to forage from blossoms of hairy vetch as trippers or as base workers where indicated.

Bee No.	Successful Visits.				Unsuccessful Visits.	
	Previously Untripped.		Previously Tripped.		No. Blos.	Sec./Blos.
	No. Blos.	Sec./Blos.	No. Blos.	Sec./Blos.		
1	21	8.1	3	5.7	3	4.7
2	23	10.3	3	8.0	8	6.4
3	34	8.0	5	4.0	10	5.0
4	26	10.6	5	4.8	4	4.1
5	10	9.2	4	4.8	4	3.8
6	23	7.5	2	4.5	6	3.2
7	19	13.7	1	5.0	6	5.8
8	15	15.3	3	13.0	2	5.5
9	12	11.2	1	8.0	0	—
10	23	12.3	4	8.2	9	5.9
11	10	12.0	2	6.0	13	4.1
12	11	8.3	2	4.5	4	4.0
Totals and Means	227	10.3	35	6.2	69	5.0
F with 11 and 215 DF		5.4 ***				
Misc. Bees	105	8.2	27	6.4	76	4.8
Base Workers	114	7.7	—	—	17	6.0

*** Probability $<$ 0.001.

Some of the visits to blossoms that the bee did not forage were difficult to classify.   A bee sometimes inserted the proboscis in to the mouth of the corolla tube and withdrew it immediately.   These visits were considered to be exploratory and were not recorded as unsuccessful attempts to trip, but sometimes there was a brief but perceptible tripping motion, especially after a bee had struggled hard and failed on one or two blossoms, or just before she returned to the hive.   Although there was some inconsistency, only the time spent on visits in which there was a definitive efforts to trip the blossoms was recorded and few of the recorded times were less than 3 seconds.   These data may, therefore, be biased slightly upward, but it is certain that bees usually spent more time in attempting to trip than in successfully tripping a blossom.

TABLE 3. — Mean number of blossoms which honeybees successfully forager per minute and per inflorescence, and the percentage of blossoms which bees unsuccessfully attempted to forage, while visiting hairy vetch, crimson clover, and hubam clover.

Legume and Year.	Type Forager.	No. Bees.	No. Min.	Blos./ Min.	Blos./ Infl.	% Unsuc.
Vetch 1953.	Trippers :					
	Pollen	4	36.2	5.1	1.8	—
	Pol. and Nect	7	117.7	4.5	1.7	—
	Nectar	9	199.1	3.0	2.7	—
	Base Workers.	6	41.7	4.6	2.1	—
Vetch 1954.	Trippers :					
	Pollen	3	15.2	3.5	2.5	32
	Pol. and Nect	19	381.7	3.2	1.8	36
	Nectar	2	49.5	2.4	1.9	28
	Base Workers.	11	132.0	4.8	2.3	9
Vetch 1955.	Trippers :					
	Pollen	2	17.0	9.1	2.4	3
	Pol. and Nect.	19	181.7	4.0	1.8	16
	Nectar	12	99.1	3.8	1.8	16
	Base Workers	5	20.5	4.9	2.1	5
All Vetch.	All Trippers	77	1097.2	3.6	1.9	—
	All Base Workers . . .	22	194.2	4.7	2.3	—
Crimson Clover.	Trippers	10	99.2	13.5	2.8	—
Hubam Clover.	Trippers	26	91.2	33.2	5.1	—

Table 3 gives a comparison in the mean over-all foraging speed of bees working on hairy vetch, crimson clover (a variety of *Trifolium incarnatum* L.), and huban clover (a variety of *Melilotus alba* Desv.).   The bees working vetch are classified according to forage gathered and the year the observations were made.   The individual bees differed widly from each other in over-all foraging speed and the samples of some types of foragers under different conditions were so small that no detailed statistical treatment of these data was attempted.   It will be noted, however, that

there is good agreement in the order of foraging speed of bees gathering the same forage in different years, and in the time required to forage individual blossoms (Table 1).

The speed with which the bees forage from the three legumes is strikingly different. During a good nectar flow when there was little competition between foragers, bees visited a mean of 38.7 hubam clover blossoms per minute and 5.9 blossoms per inflorescence (WEAVER et. al., 1953). During a poorer flow in 1955 when there was much more competition between foragers, bees spent more time on the wing and visited a mean of 29.5 blossoms per minute, and 4.6 blossoms per inflorescence. Blossoms of the clovers are much smaller and more easily tripped and worked than vetch blossoms; bees reach the nectary of hubam clover with ease, and of crimson clover with some difficulty. The hubam clover blossom is foraged so quickly that no attempt was made to determine the length of time required to forage from individual blossoms. According to 79 observations a mean of 3.4 ± 0.2 seconds was required for a bee to forage from a crimson clover blossom. Computations from this figure and the mean number of blossoms foraged per minute indicate that the bees spent 76 per cent of their time foraging from blossoms and the remainder of their time at other activities, mainly in exploring blossoms, packing pollen on the corbiculae, or doing both simultaneously. Similar computations from the data in Tables 1 and 3 indicate that in 1955 the different types of foragers spent means of from 66 to 69 per cent of their time in successfully foraging from vetch blossoms, and the remainder of their time at other activities. Less than 6 per cent of the time was spent in unsuccessfully attempting to forage from blossoms. These data were taken over a fairly homogeneous period in the condition of vetch plants and in the nectar flow. It is doubted that the agreement would have been as close if the data had been taken over more varied conditions, and it is certain that a far smaller percentage of the time is spent in foraging from blossoms during a poor nectar flow.

The trippers gathering nectar only seem to represent two types of foragers. During fast nectar flows when colonies gathered from 6 to 17 kg. of nectar a day, there was little difference in the mean foraging speed of trippers foraging for nectar only and those gathering both nectar and pollen, but after several days with a poor flow the few nectar gathering trippers remaining in the field were invariably highly inefficient workers that visited a mean of at least one fewer blossoms per minute than the mean of the bees gathering both nectar and pollen. It may be that their failure to pack the pollen that clung to their bodies was another expression of their inefficiency. It is believed that after the nectar flow deteriorated most of the efficient and some of the inefficient tripping nectar gatherers ceased to forage, began to gather both pollen and nectar, or became base workers, and that the failure to make a change was a symptom of a general inefficiency.

The slower foragers seemed to be more prone to revisit blossoms that

they had previously tripped than the faster workers, and to be less aware of their surroundings. To keep a bee's performance in clear view it was necessary to get very close to her, and sometimes the observer, while pushing aside entwining vines, shook the raceme being foraged. Of nine bees followed for over 40 minutes, six foraged at less than the mean speed and two at the mean speed, for their own type and year. Prolonged observations on slow bees may have biased the data slightly in favor of the more inefficient foragers, but this was counterbalanced to an unknown extent by the impossibility of prolonged observations on bees that spent most of their time exploring. Many of the highly efficient foragers appeared nervous in their activities, though a few simply went about their tasks in a businesslike way with little lost motion.

Aside from the variation in the speed of work of the bees, there were differences in the ease with which different blossoms were tripped, and some of these differences seem to have been related to the temperature during bud development. The blossoms that developed during cool weather appeared to be slenderer and more difficult to trip than those that developed during warm weather. The average temperature in May 1954 was more than 2°C. cooler than May 1953 and 3°C. cooler than May 1955. Many more of the observations in 1954 followed the cooler weather than in 1953 or 1955. No records were kept in 1954 on the time required for bees to trip or work individual blossoms, but the slow over-all foraging speed of trippers that year appeared to be due to the greater time and effort required by the bees to trip the blossoms, and the larger percentage of blossoms that they were unable to trip. As indicated above, the data on unsuccessful visits depended upon subjective decisions by the observer, and some of these decisions were undoubtedly inconsistent with each other. The percentages of unsuccessful visits in Table 3, however, do indicate the magnitude of difference in 1954 and 1955. Since honeybees are dependable pollinators of alfalfa in parts of California, but not in Manitoba (STEPHEN, 1956), it is suggested that a temperature dependent difference in the ease with which the blossoms are tripped might be partially responsible for this variation.

Some bees spent a great deal of time hovering near, crawling over, and inserting the tongue quickly into blossoms of both vetch and crimson clover. These appeared to be exploratory activities which probably depended upon the sense of smell and the perception of water to locate nectar, and possibly upon tactile and visual senses to distinguish blossoms mature enough to trip easily. These exploratory activities would probably be to the bees' disadvantage when visiting blossoms in which the nectar or pollen is quickly and easily reached, since the time and energy spent in this manner might exceed that required to reach the nectary or anthers, but if exploration resulted in a higher percentage of the blossoms being fruitfully visited, it would be to the bees' advantage on crops that are difficult to forage. Some observations indicated that the ability or inclination to perceive differences in blossoms is not highly developed in all

individuals.   Some bees often attempted unsuccessfully to trip older buds; a few bees worked virtually no blossoms that had not previously been tripped; and a few bees often reworked blossoms 1 to 3 times before leaving a raceme, or returned to a previously visited raceme and reworked the blossoms; one base worker and one nectar and pollen gatherer were observed visiting only partially withered blossoms.   The more inefficient foragers (as determined by the mean number of blossoms foraged per minute) appeared to spend less time exploring and more time revisiting previously tripped blossoms than the more efficient foragers.   In spite of the probable disadvantage to the colony of activities of this kind the ability to locate a likely source of nectar or pollen without contact with it is probably of greater selective advantage to the colony as an aid in finding new forage than in choosing individual blossoms of a species to work.

Some colonies of honeybees are superior to others as nectar gatherers, and the superiority is not fully explained.   It is postulated that certain aspects of foraging behavior, and some physiological mechanisms which affect foraging behavior are heritable, and that colonies of bees differ in the mean foraging ability of their workers; all else being equal, the colony with the most efficient foragers will gather the most nectar and pollen.

Summary.

The foraging area of a bee is small during a good nectar flow, but as the nectar flow deteriorates the foraging area becomes larger, the bee begins to explore further from her original, area, and is less persistent in her efforts to trip blossoms.   If the flow improves again, or remains fairly constant, the bees become more settled in their foraging behavior.   An interruption of foraging probably makes it easier for a bee to be recruited to a new area completely removed from the old one.   It appears that attack on other bees probably aid in keeping a foraging area free of too much competition from other bees.   During a period when the nectar flow fluctuated rather widely, bees moved more than 15 cm. on less than 50 per cent of their flights, and more than 100 cm. on only about 4 per cent of their flights.   There were rather minor differences between trippers and base workers in the frequency with which flights of some distances occurred.

Bees gathering the same forage differed from each other in the mean time required to forage from individual blossoms.   Of bees gathering different forage, or foraging in different ways, pollen gatherers foraged blossoms the fastest, base workers next, pollen and nectar gatherers next, and tripping nectar gatherers the slowest.   The over all foraging speed of the bees fell in the same order, and the data indicated that bees spent approximately 65 to 70 per cent of their time foraging from blossoms, and the remainder of their time at other activities.   There was great variation in the over all foraging speed of individual bees, and in the ease with

which different blossoms were tripped. It is proposed that temperature dependent differences in the ease with which blossoms are tripped may account for some of the variability in the value of bees as pollinators of certain crops. During fast nectar flows there was little difference in the foraging speed of tripping nectar gatherers and bees gathering both nectar and pollen, but after several days with a poor nectar flow the few remaining nectar gatherers were inefficient foragers. The inefficient workers were more prone than efficient ones to revisit previously foraged blossoms, and they spent little time exploring. It is proposed that differences in the foraging efficiency of bees help to account for differences in honey production by colonies.

Sommaire.

L'étendue du vol d'une Abeille quand elle va butiner n'est pas grande pendant que le nectar est abondant, mais, quand le nectar devient rare, l'Abeille commence à explorer de plus en plus loin de sa région de butinement originelle et elle est, de plus, moins persistante dans ses efforts de « trip » les fleurs. Si la miellée devient plus grande encore ou si elle reste à peu près constante, l'Abeille devient plus régulière dans la conduite de son butinement. Une interruption de butinement facilite probablement le déplacement de l'Abeille vers une nouvelle région bien éloignée de sa région originelle. Il paraît que les assauts contre les autres Abeilles aident probablement à maintenir une région de butinement libre de trop de concurrence des autres Abeilles. Pendant une période, quand la miellée fluctuait beaucoup, les Abeilles volaient plus de 15 cm sur à peu près 50 p. 100 de leurs vols et plus de 100 cm sur à peu près 4 p. 100 de leurs vols. Il y avait de petites différences entre les Abeilles qui « trip » les fleurs et les ouvrières qui butinent à la base des fleurs en ce qui concerne le nombre de vols de grande étendue.

Les Abeilles butinant dans les mêmes fleurs ne se sont pas accordées sur le temps moyen de butiner dans des fleurs individuelles. En ce qui concerne la vitesse de butiner des Abeilles qui butinent dans des sources de nectar variées, ou de celles dont la façon de butiner varie, celles qui recueillent le pollen butinent le plus vite, puis les ouvrières de base, ensuite celles qui recueillent et le pollen et le nectar, et, enfin, celles qui « trip » sont les moins vites. La vitesse de butiner hors tout des Abeilles est du même ordre, et les données indiquent que les Abeilles passent à peu près 70 p. 100 de leur temps à butiner des fleurs et le reste de leur temps à faire autre chose. Il y avait une grande variation dans la vitesse hors tout d'une Abeille individuelle et dans la facilité de « trip » des fleurs. Il se propose que les différences dépendant de la température dans la facilité de « trip » les fleurs pourraient expliquer en quelque façon la variabilité de la valeur des Abeilles en tant que pollinisateurs de certaines plantes. Pendant les miellées rapides, il y avait peu de différence entre la vitesse de butiner des Abeilles-trippers qui recueillent le nectar et les Abeilles recueillant et le nectar et le pollen ; mais, après

plusieurs jours d'une pauvre miellée, les quelques Abeilles qui continuaient à recueillir le nectar étaient inefficaces dans leur butinement. Les ouvrières inefficaces étaient plus enclines que les efficaces à visiter encore une fois les fleurs préalablement visitées et elles ont passé peu de temps à explorer. Il se propose que les différences dans l'efficacité des Abeilles aident à expliquer les différences dans la production de miel dans les diverses colonies.

Zusammenfassung.

Bei reichlicher Nektartracht ist das Sammelgebiet einer Biene klein, aber wenn die Tracht weniger ergiebig wird, erweitert sich das Gebiet; die Biene unternimmt dann Entdeckungsflüge nach entlegeneren Feldern und ist weniger bestrebt, die Blüten aufzuschnellen. Wenn die Tracht wieder besser wird oder auf gleicher Höhe bleibt, wird die Tätigkeit der Bienen gleichmäßiger. Es ist möglich, daß eine Unterbrechung der Sammeltätigkeit die Umstellung einer Biene auf ein neues, vom alten völlig getrenntes Sammelgebiet erleichtert. Es scheint, daß Angriffe auf andere Völker dazu beitragen, das Sammelgebiet von einem Übermaß von Konkurrenten freizuhalten. Als die Ergiebigkeit der Tracht stark schwankte, flogen die Bienen weiter als 15 cm bei weniger als 50 v. H. ihrer Flüge, und weiter als 100 cm bei unter 4 v. H. ihrer Flüge. Schnellerinnen und Bodenarbeiterinnen unternahmen ungefähr die gleiche Anzahl von Flügen über größeren Strecken.

Die zum Besuch einer einzelnen Blüte erforderliche Durchschnittszeit schwankte bei Bienen, die die gleichen Nahrungsarten sammelten. Von den Bienen, die verschiedenartige Nahrung, oder die Nahrung auf verschiedenartige Weise sammelten, arbeiteten die Pollensammlerinnen am schnellsten, dann die Bodensammlerinnen, die Pollen- und Nektarsammlerinnen, und schließlich die Schnellerinnen. Die Gesamtbeflugsgeschwindigkeit der Bienen folgten in derselben Reihenfolge, und die Beobachtungsergebnisse zeigen, daß die Bienen ungefähr 70 v. H. ihrer Zeit mit dem Beflug der Blüten zugebracht haben, und den Rest der Zeit mit anderen Tätigkeiten verbracht. Die Gesamtbeflugsgeschwindigkeiten der einzelnen Bienen schwankten stark, und ebenso die Leichtigkeit mit der die verschiedenen Blüten aufgeschnellt wurden. Die Annahme liegt nahe, daß temperaturbedingte Verschiedenheiten in der Leichtigkeit, mit der die einzelnen Blüten aufgeschnellt werden können, der Grund für die verschiedene Leistungsfähigkeit der Bienen als Befruchtungsvermittlerinnen bei den einzelnen Kulturpflanzenarten sind. Bei ergiebiger Nektartracht zeigten sich nur geringe Schwankungen in der Sammelgeschwindigkeit der aufschnellenden Nektarsammlerinnen und der sowohl Nektar als auch Pollen sammelnden Bienen, aber nach ein paar Tagen mit geringer Nektartracht zeigten die wenigen übriggebliebenen Nektarsammlerinnen einen unrentablen Energieverbrauch. Die « unrentablen » Arbeiterinnen neigten mehr dazu, schon beflogene Blüten wieder zu besuchen, als die wirksam arbei-

tenden Bienen. Erstere wandten auch weniger Zeit auf Entdeckungsflüge an. Es ist anzunehmen, daß die Verschiedenheiten in der Leistungsfähigkeit der Sammelbienen, wenigstens zum Teil, die Verschiedenheiten in der Honigerzeugung bei den verschiedenen Bienenvölkern erklären.

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II

NOUVELLES DE L'UNION

LISTE ALPHABÉTIQUE DES MEMBRES DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX

Le Secrétariat présente ci-dessous la liste alphabétique de tous les membres actuels de l'U. I. E. I. S.

Pour chaque membre, l'ordre suivi pour les divers renseignements donnés est le suivant :

NOM (Prénom). — Titre. — Adresse. — NATIONALITÉ. — *Spécialités*.

Abréviations de nationalités

AN. Angola.
AR. Argentine.
BE. Belgique.
BR. Brésil.
CA. Canada.
DA. Danemark.
DE. Allemagne.
FR. France.
GB. Grande-Bretagne.
IN. Inde.
IS. Israël.
IT. Italie.
JA. Japon.
LU. Luxembourg.
NE. Hollande.
SA. Afrique du Sud.
SR. Sarre.
SW. Suède.
SZ. Suisse.
U. S. A. États-Unis d'Amérique.
U. S. S. R. Union soviétique.

Abréviations de spécialités.

Ac. Acridoidea.
Ap. Apoidea.
I. Isoptera.
F. Formicoidea.
Hy. Hymenoptera, en général.
My. Myrmecophiles.
Te. Termitophiles.
V. Vespoidea.
I. S. Insectes sociaux, autres que les groupes précédents.
P. S. Phénomènes sociaux en général.
Ph. I. S. Physiologie des Insectes sociaux.

Il manque dans cette liste quelques indications de spécialités ; il peut manquer aussi quelques noms de membres de l'Union. Le Secrétaire prie tous ceux qui relèveront des erreurs de l'en excuser, et c'est avec reconnaissance qu'il recevra toutes les critiques ou les rectifications qui s'imposent.

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American Museum of Nat. Hist., library, Central Park West at 79th. Street, *New York 24*, U. S. A.
Argus de la Presse, 37, rue Bergère, *Paris-IX*e.
Bibliothèque de C. N. R. S., 13, quai Anatole-France, *Paris-VII*e.
Bibliothèque du Laboratoire d'Évolution, 105, boulevard Raspail, *Paris-VI*e.
Bibliothèque nationale, Régie du dépôt légal des périodiques, rue Richelieu, *Paris*.
Bibliothèque de la Station Biologique des Eyzies, *Les Eyzies* (Dordogne). France.
Bibliothèque de l'Université, *Lund*, Suède.
Brooklyn College library, Bedford avenue and avenue H, Brooklyn, *New York*, U. S. A.
Centre d'Études du Bouchet, Vert-le-Petit (Seine-et-Oise).
Établissement fédéral d'industrie laitière, Section Apiculture, *Liebefeld-Berne*, Suisse.
Flory Jean, bibliothécaire, 13, rue de Buci, *Paris-VI*e.
Harvard University library, *Cambridge*, Massachusetts, U. S. A.
Harvard Tilton memorial library, Audubon Place and Freret Street, *New Orleans*, Louisiana, U. S. A.
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Institut Royal des Sciences naturelles de Belgique, Entomologie, 31, rue Vautier, *Bruxelles*.
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Library, Oregon state College, *Corvallis*, Oregon, U. S. A.
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National Institutes of Health, library, *Bethseda*, Maryland, U. S. A.
Office of the Forest research institute and Colleges, P. O., *New Forest* (Dehra Dun), U. P. India.
Ohio State University, library, *Columbus 17*, Ohio, U. S. A.
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Statens=Biavlsforsög « Strödam », Hillerod, DA.
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University of Kansas, Periodical Depart. library, *Lawrence*, Kansas, U. S. A.
University of Minnesota, library, *Minneapolis*, Minnesota, U. S. A.
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THE THIRD ANNUAL MEETING OF THE JAPANESE SECTION IN FUKUOKA

(October 20. 1956).

The third annual meeting of the Japanese Section was held, in conjunction with the annual meeting of the Zoological Society of Japan in Fukuoka at "Keiaien"-Hall of the Faculty of Medicine, Kyushû University. The meeting was called to order by Prof. Tohru UCHIDA, President of the Section, at 16.50. In the absence of the Secretary, Mr. R. Ohgushi served as chairman pro tem. There were present only five members of U. I. I. S., but 13 guests as follows:

Members: KUWABARA (M.), MORISITA (M.), OHGUSHI (R.), UCHIDA (T.), YOSHIKAWA (K.).

Guests: FUJIMOTO (Y.), FUKAMACHI (U.), HONJO (I.), IKUSHIMA (K.), KAWABATA (M.), KIKUCHI (T.), KUBO (Y.), MIYOSHI (R.), MURAKAMI (Y.), NISHIYAMA (I.), NOMURA (K.), ONO (Y.), YANAGIDA (T.).

Chairman: Mr. OHGUSHI.

Management: Mr. KAWOBATA, Mr. ONO (not' the members of U. I. I. S. but served with kindness).

A. **Business Meeting** (16.50 - 17.30).

1. After the brief report of the general affairs during the year, the chairman demanded for members the more vivid sending of manuscripts to "Insectes Sociaux", and of the abstracts of their annual works to the Secretariat. Several administrative problems were discussed among the members.

2. On the place and time of the Annual Meeting, it was decided that the Meeting ought to be held always in conjunction with the Annual Meeting of the Zoological Society of Japan. Because of the absence of Prof. Tsuneki of Fukui University (locatateed nea Kanazawa where the next Annual Meeting of the Z. S. J. is held), and the secretary, no decision was given respect to the exact plan of the next Annual Meeting.

3. The standarization of technical terms was proposed by the chairman, but no concrete opinions were presented.

B. **Lectures** (17.30 - 18.30).

1. KUWABARA (M.). — Individual and group in honeybee. Discussions between the lecturer and Mrs. Ohgushi, Uchida, Kawabata, Honjo, Morisita, Fujimoto, Yoshikawa and Ono.

2. MORISITA (M.). — Sociality and Individuality among animals.

The lectures ended on 18.30.

C. **Dinner** (18.30 - 19.30).

TRAVAUX PUBLIÉS PAR DES MEMBRES DE L'UNION

1954. Itô (M.). — **Experimental studies on the mechanism of aggregation formation with special reference to the border effects of movement of the red-rust flour beetle** (*Physiol. & Écol.*, **6** (1), 55-62, in Japanese with English résumé). A study on the mechanism of aggregation formation in *Tribolium castaneum*, with reference to the change of aggregation degrees under different environmental conditions. Three main causal factors were discovered. 1. Sexual attraction among animals, 2. Non-sexual attraction, 3. Border effects. The outermost zone of the exp. field always gave higher frequency values than inner zones. This border-effects cannot be fully explained by the thigmotactic concepts, and will be served for the evaluation of the behavioral coaction of the social insects.

1955. — **On the meaning of the « air-space » in the population growth of the red-rust flour beetle,** *Tribolium castaneum* (Herbst), (*Oyô-Kontyû*, **11** (1), 25, in Jap. with English résumé). The ecological significance of the « air-space » above flour for the population increase, esp. for the oviposition behavior was examined. Some significance against the adult behaviors such as courtship, copulation and burrowing were observed, but without the functional differentiation of chambers as in some bark-beetles. Comparing the differences betw. « air-space » and non air-space » blocks, the former exceeds in the no of eggs deposited, max. oviposition numbers etc. after five days from the start.

1955. — **Basic properties of social insects. On the group effect observed in certain gregarious insects, from the view point of the comparative sociology.** (*Biol. Sci.*, **7**, (2). 67, in Japanese.)

1955. Iwata (K).. — **The comparative anatomy of the ovary in Hymenoptera. Part I. Aculeata** (*Mushi*, 29, (4), 17-34, English) In connection with the habits of female Aculeata, the number of ovarioles, of mature and immature oocytes etc. were studied with 160 spp. of Aculeata, including 13 spp. of Formicidae, 10 spp. of social Vespidae, and 4 spp. of social Apidae.

1956. — **Insects and their nests, iii-251 pp. with 8 plates** (Rikusuisha, Tokyo, in Japanese). A comprehensive treatise on various types of nests found among insects. The book is consisted of the following eleven chapters: 1. Houses and nests, 2. Insects which build no nests, 3. Insects which hide themselves in food, 4. Insects which build nest since immature stages, 5. Insects depositing their progeny in the nest of other species, 6. Insects which build the nest and store the food for their own progeny, 7. Insects which utilize the ability of other species for their own progeny, 8. Insects which provide successively the food for their own progeny in the nest, 9. Insects which utilize their daughters' ability for nesting and brood-rearing, 10. Insects which utilize the ability of other species for nesting and brood-rearing, 11. Supposed history of the development of nests. The subsocial and social insects are treated mainly in chapters 7 - 9 but occasionally also in others. The book is written based upon the author's rich experience obtained during several decades and contains numerous original considerations.

1954. Kuwabara (M.)., Maeno (T.), Matsunaga (T.). — **Relative stimulating effectiveness of various cations on the chemoreceptors of mouth part in the honeybee,** *Apis mellifera* (*Physiol. & Écol.*, **6**, 40, in Japanese with English résumé). With various cations, relative stimulating effectiveness was investigated on the chemoreceptors of mouthpart of the honeybee. Chlorides were used as the test compounds, and the rejection threshold concentrations in M/4 sucrose solution were determined. Taking the reciprocal of rejection threshold as a criterion for measuring the effectiveness of stimulation, the following series was obtained : $Li^+ < Na^+ = K^+ < NII^+ < Mg^{++} = Sr^{++} = Ba^{++} < Ca^{++}$. The series is similar to that concerned with the acceleration of the swelling of gelatine. it seems to be correlated with the lyotropic series.

1956. Sakagami (Sh. F.). — **Zur Wahrnehmungspsychologie der optischen Dressur bei der Honigbiene. Beitrag I : Dressierbarkeit gegen konturarme Figur gestellt auf konturreichem Grund** (*J. Fac. Sci., Hokkaido Univ.*, Ser. VI, Zool., **12**, 333-361). Ein bis heute tatsächlich erfolglos gebliebener Versuch, die Dressur der Biene auf die konturarme Gliederung gegen die konturreiche, wurde durch Verwendung der ausgetauschten Figur und Grund Beziehung ausgeführt. Dressur der Biene mit Futterglas auf Situation Kreis/Muster erfolgte in gelbem Kreis sehr leicht u. sicher, in schwarzem Kreis, dagegen sehr labil, und nur dann, wenn das Futterglas gleichzeitig dargeboten wurde. Erst durch direkte Futterung auf Glasplatte suchten die Bienen zieltreu Kreis/Muster. Kontrollversuche bewiesen, daß selbst die absolute Primärtendenz zur konturreichen Struktur, sogar nach Bildung der Dressur auf Kreis/Muster, nicht verloren, sondern durch Reizkonstellation nur gehemmt ist. Die räumlichen u. zeitlichen Auflösungen der Biene in der Versuchssituation analysiert. Einige Erörterungen über die Wahrnehmungsorganisation ihres Sehfeldes gegeben.

1953. Shida (T.). **Seven years with** *Vespula lewisii*, I (*Hachi*, No. **8**, 1. in Japansese, mimeographed). The males leave their nest in the end of autumn. In this period, their stomach is filled with a plenty of honey which may serve as a energy source during his automnal flight. The fulfilment of stomach proceeds in correlation with the development of reproductive organs. Both the processes are completed before leaving from their nest. This fact explains why they cannot find abundantly on the flowers, in contrast to the male of *Dolichovespula*, and why they can fly about actively without accumulated fat-bodies.

1849. Takamatsu (Y.). — **Studies on Vespula lewisii** (Cameron) III. **On the nest-leaving of the new queen at the latter part of autumn.** (*Physiol. & Écol.*, **3**, 38, in Japanese with English résumé). During the autumn of 1947, the measurement of nest temperature was undertaken with a large nest of *V. lewisii*. Means of max. & min. daily temperature during the obs., were $15°.94^{00}$ and $-1°.93°$ C in outdoor and $13.43°$ & $3.45°$ cin the nest. The nest-leaving of new queens was taken place mostly betw. 10.00 - 13.00 (93.7 %). In all 874 leaved queens during. 21 days, no orientation flight and returning to their nest were observed.

1951. — **Studies on... IV. On the quantitative relations, with reference to sex, between the length and weight of the body and the length of the wing in all members constituting one nest** (*Pysiol. & Écol.*, **4**, 102-104, in Japanese with English résumé). From the measurements on all members constituting one nest ($♀$ 190, $♂$ 610, $♀$ 825 at November), the following results were obtained: 1. Relative values among body length, body weight and wing length are in good agreement with the behaviors of the queen, drone and worker. 2. In later autumn, ratio (body weight/body length) is largest in queens and smallest in workers, which accords with anatomical evidences as well as with ecological fates of three castes.

1951. — **Studies.. V. On the form and histological structure of the central nervous system** (*Bull. Fac. Agric., Shinshu Univ.*, No. **1**, 57-67, in Japanese with English

résumé). Descriptions of the general structure of nervous system in larvae and adults, especially with detail histological observations of the brain.

1952. — **Studies on the mechanism of the determination of the sexual function in** *Vespula lewisii* (Cameron) (*J. Fac. Agric. Shinshu Univ.*, No. **2**, 1-46, in Japanese with English résumé). Differences btw. queen and worker ovaries were described. Well developed follicular cells and oocytes in queen ovaries show a sharp contrast to remarkablly atrophied worker ones. Corpora allata increase its volume during metamosphosis, but decrease distinctly at the pupal stage. Rate of decrease is largest in drone and smallest in queen. Hence the relative size of the organ among three castes is 6.78 (♀): 1.38 (♀): 1 (♂). This order represents simultaneously the degree of activities observed histologically. Various ligation and decapitation experiments were performed.

1955. TANIGUCHI (S.). — **Biological studies on the Japanese bees II. Studies on the nesting behaviour of** *Bombus ardens* Smith. (*Sci. Rep. Hyogo Univ. Agric.*, 2, Ser. *Agric.* **89**). The first record of the nest of *B. ardens*. The nesting life of this species ends early in July. The following items were observed. 1. Behaviour of foragers and new females (diurnal rhythm of foraging, behaviour in departure and return, density of trips in a day time, behav. of marked individuals, pollen-roads, the last day of workers). 2. Males and the copulation of new females. 3. Flower visited by *B. ardens*.

1955. UCHIDA (T.), SAKAGAMI (Sh. F.). — **The seasonal population-trends of the honey-bee in Sapporo, with some remarks on supersedure** (*Jap. J. Zool.*, **11**, 55). The seasonal changes of population number in three colonies were illustrated by Bodenheimer's method with minor modifications. Because of the colder climate in Sapporo, the seasonal shift of pop. growth was clear when compared with Bodenheimer's results in Jerusalem and Nolan's one in Baltimore. In all cases the supersedure occured after the pop. peak was attained in June or July, but in two colonies a two-peak curve was obtained caused by the autumnal recovery. From a close correlation between formation of royal chambers and lowered brood/nurser ratio, it was assumed that the overpopulated nursers for the decreased broods seemed to be one of the important factors to evoke the supersedure (or swarming). Finally, the importance of the further studies on the longevity estimation was emphasized by illustrating a marked difference in total pop. number resulted by two different estimations.

1952. UTIDA (S.). — « **Phase** » **dimorphism observed in the laboratory population of the cowpea weevil,** *Callosobruchus quadrimaculatus* (*Oyô-Dobuts. Zasshi*, **18**, 161-168, in Japanese with English résumé). In the laboratory population of the cowpea weevil, dimorphic forms were found out. They differ each other in body form, abdominal structure, color, indiv. variation in the body size, movement, duration of adult life, adult body weight when emerged, number of eggs deposited, death feigning and heat resistance. These dimorphic forms seem to arise from the influence of environment and not due to genetical cause. Some experiments support the explanation that these forms are caused by the difference of the density effect operating in the period of larval development (After Author's summary). It seems to be suggestive to the social dimorphism of the social insects that the phenomenon resembling to the « phase » variation was observed depend on the pop. density in any biol. characters of insects (by M. Itô).

1952. — **Space of iso-effect of density** (*Research on Pop. Écol.*, **1**, 119-121, in Japanese with English résumé. Some conceptions in the pop. ecology is here proposed to understand clearly the pop. phenomenanin a heterogeneous environment. To test the homogeneity of an environment, the density effects is used, and the space of

iso-effect of density is termed as an unit space fort the measurement of density. In this space, the Pearl-Verhulst coefficient h takes a constant value. Against to the crude density, we call this density as the *eco-density* (after Author's summary). The conceptions will be served for qualitative evaluation of the social character of insects (by M.Itô).

1955. YOSHIKAWA (K.). — **A polistine colony usurped by a foreign queen. Ecological studies of Polistes wasps, II.** (*Ins. Soc.*, **1**, 255-260). Observations on the usurpation of a colony of Polistes fedwigae D. T. by another fecundate queen of superindividual stage. Modes of attack for two colonies and the defense by the latters were described. Some considerations were given with respect to the difference btw. the observed phenomenon and socalled social or labour parasitism.

WAY (M. J.), SYNGE (A. D.). — 1948. **The effects of D. D. T. and Benzene Hexachloride on bees.** (*Ann. appl. Biol.*, **35**, 94-109.)

Although it was demonstrated in the laboratory that D. D. T. in fairly high concentrations acts as a contact poison to bees and also as a stomach poison that is rather more toxic than lead arsenate, it was found that in the field the commercial preparations of D. D. T. that were tested by application to open blossom are apparently harmless to foraging bees.

Laboratory experiments showed that Benzene Hexachloride is a powerful contact and stomach poison to honeybees and bumblebees, and the results of field experiments with commercial preparations confirm its potential danger to foraging bees.

WYKES (G. R.). — 1951. **Selection of certain nectars by honeybees.** (*Ann. Rep. Cent. Assoc. Brit. B. K. Assoc.*)

A discussion of various factors which affect the taste perception of honeybees and their selective nectar gathering behaviour when foraging.

WYKES (G. R.). — 1952. **An investigation of the sugars present in the nectar of flowers of various species.** (*New Phytol.*, **51**, 210-215.)

Quantitative determinations were made of nectar sugars by means of paper chromatography. In nectar obtained from 61 species sucrose, glucose and fructose were present in all but one sample. In addition, maltose and two other sugars of low RF values were found in the nectar of some species.

WYKES (G. R.). — 1952. **The influence of variations in the supply of carbohydrate on the process of nectar secretion.** (*New phytol.*, **51** (**3**), 294-300..)

The supply of carbohydrate available to nectar-secreting flowers was varied by different treatments and the influence of such variations on the amount and sugar concentration of nectar secreted was determined. Application of ringing and defoliating treatments to flowering shoots showed that the supply of carbohydrate may become a limiting factor for nectar secretion. In a series of sugar-feeding experiments it was found that the concentration of nectar and the amount of sugar secreted varied directly with the sugar concentration of the feeding solution, whereas the weight of nectar did not. Differences in the kinds of sugars supplied did not appear to influence nectar content.

WYKES (G. R.). — 1952. **The preferences of honeybees for solutions of various sugars which occur in nectar.** (*J. exp. Biol.*, **29** (**4**), 511-518.)

When bees were offered equal volumes of sugar solutions, of different composition but the same total concentration, in laboratory and field experiments, it was found that sugars which occur in nectar are not equally attractive to them. Consistent preferences were shown for solutions of single sugars in the following descending order; sucrose, glucose, maltose, fructose. The acceptances of some mixtures differed from those predicted on the basis of an additive effect of the constituent sugars in

single solution.   High preferences were shown for the sucrose-glucose-fructose solutions.

No direct relationship appears to exist between the chemical constitution of the sugars offered and their acceptance by bees, and no adequate explanation can be offered for the observed differences in preferences for solutions of either single or mixed sugars.

The possible biological significance of such selective responses by bees is discussed.

WYKES (G. R.). — 1953. **The sugar content of nectars.** (*Biochem. J.*, **53**, 294-296.)

The sugars present in nectar secreted by twelve species of plants were separated on paper chromatograms, and quantitative determinations were made of the glucose and fructose present.   It was found that the proportions of glucose and fructose varied greatly in nectar from the different species, but, for any one species, the proportions of these sugars appeared to remain relatively constant.

Studies in Pharaoh's ant, Monomorium Pharaonis (L.)

1949. PEACOCK (A. D.), BAXTER (A. T.). — **The Rearing of Artificial colonies.** (*Ent. mon. Mag.*, **85**, 256-260.)

1950. PEACOCK (A. D.). — **Methods of Recording Observations on Artificial Colonies.** (*Ibid.*, **86**, 129-135.)

1950. PEACOCK (A. D.), BAXTER (A. T.). — **Life History.** (*Ibid.*, **86**, 171-178.)

1950. PEACOCK (A. D.). — **Egg-Production.** (*Ibid.*, **86**, 294-298.)

1951. PEACOCK (A. D.). — **Pupal and Adult Sex Ratios.** (*Ibid.*, **87**, 185-191.)

1951. HALL (D. W.), SMITH (I. C.). — **External Characters, Size variation and Cephalic Ratios.** (*Ibid.*, **87**, 217-221.)

1952. HALL (D. W.), SMITH (I. C.). — **Thoracic Structures, Typical and Atypical.** (*Ibid.*, **88**, 97-102.)

1954. PEACOCK (A. D.), SMITH (I. C.), HALL (D. W.), BAXTER (A. T.). — **Male production by Parthenogenesis.** (*Ibid.*, **90**, 154-158.)

1954. HALL (D. W.), SMITH (I. C.). — **Somatic Mosaics.** (*Ibid.*, **90**, 176-182.)

1955. PEACOCK (A. D.), WATERHOUSE (F. L.), BAXTER (A. T.). — **Viability in regard to Temperature and Humidity.** (*Ibid.*, **91**, 37-42.)

1955. PEACOCK (A. D.), SUDD (J. H.), BAXTER (A. T.). — **Colony Foundation.** (*Ibid.*, **91**, 125-129.)

1955. PEACOCK (A. D.), SUDD (J. H.), BAXTER (A. T.). — **Dissemination.** (*Ibid.*, **91**, 130-133.)

1950. PEACOCK (A. D.), HALL (D. W.), SMITH (I. C.), GOODFELLOW (A.). — **The Biology and Control of the Ant Pest** *Monomorium pharaonis* (L.). (*Dept. Agric. Misc. Pub.*, **17**.)

1950. PEACOCK (A. D.). — **Pharaoh's Ant, A Pest of Hospitals and Other Premises.** (*Dept. of Health for Scotland "Health Bulletin"*, vol. **8**, n° 4.)

1953. HALL (D. W.), SMITH (I. C.). — **Atypical Forms of the Wingless Worker Female in** *Monomorium pharaonis* (L.) (**Hymenoptera:Formicidae**). (*Evolution*, 7, n° 2.)

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